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PRIMARY SUCCESSION AND PLANT PATTERN DEVELOPMENT ON PROGLACIAL DEPOSITS IN THE CANADIAN ROCKY MOUNTAINS

by

DANIEL A. MacISAAC (C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled PRIMARY SUCCESSION AND PLANT PATTERN DEVELOPMENT ON PROGLACIAL DEPOSITS IN THE CANADIAN ROCKY MOUNTAINS submitted by Daniel A. MacIsaac in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in Plant Ecology

Mark Dale
Supervisor

Supervisor

G. P. Kershaw

Date October 12, 1989

To my loving wife, Linda.

ABSTRACT

Primary succession and plant pattern development were studied at two calcareous subalpine sites in the main ranges of the Canadian Rocky Mountains: (1) Moraines adjacent to the Southeast Lyell Glacier, Banff National Park (51° 54′ N, 116° 58′ W, 1600 m); (2) Glaciofluvial outwash adjacent to the Dome Glacier and Sunwapta River at the Columbia Icefield, Jasper National Park (52° 13′ N, 117° 14′ W, 2000 m).

Hypotheses were tested at these sites concerning three phenomena: (1) Plant Pattern Development, (2) Nucleation and (3) Plant Community Development. (2 & 3 at Southeast Lyell site only).

The Southeast Lyell site represents a well-developed primary vegetation chronosequence, developing from open *Dryas drummondii* communities to closed *Picea engelmannii* forest communities. At the Columbia Icefield site, the succession appears to be restricted to a cyclical succession of *Dryas drummondi*, due to higher elevation.

There is some evidence for nucleation by *Dryas drummondii* and its role in quantitative facilitation during succession. Most of the evidence suggests, however, that surface stability (autogenic control) is the major factor in establishment of both *Dryas* and longer-lived woody species.

The observed changes in pattern during primary succession are consistent with the model of pattern development as proposed by Greig-Smith and modified by Yarranton and Morrison. Scale generally increases with time and intensity is greatest on intermediate-aged surfaces. Several scales of pattern are observed, related to species morphology and larger scale environmental control.

Both vegetation and pattern complexity are greatest on intermediate-aged surfaces.

There are five discernible seral stages in the Southeast Lyell sere, with the following association names: 1. incipient *Dryas drummondii* (0-10 years) 2. *Dryas drummondii* (20-50 years) 3. *Picea engelmannii/Dryas drummondii* (50-90 years) 4. *Picea engelmannii/Shepherdia canadensis* (125-145 years) 5. *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens* (>432 years, old-growth forest).

At the Southeast Lyell site, the old-growth forest is the most diverse community, in species richness, evenness and species diversity. Plant community development within the trimline at the Southeast Lyell study site proceeds in a predictable unidirectional sequence.

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1 INTRODUCTION

1.1 Background

Plant succession is of great interest to ecologists, and a source of much debate, partly because the concepts are not universally agreed on. The word "succession" comes from the Latin meaning "the act of coming one after the other in order of sequence". In an ecological context, Connell and Slatyer (1977) define it as "... changes observed in an ecological community following a perturbation that opens up a space". This is the definition that is used in this research.

Clements (1916) was one of the first to distinguish between primary and secondary succession. Primary succession is initiated on unstructured material which has never supported plant cover. Processes causing primary succession include land slides, deglaciation, volcanism and anthropogenic disturbance. Secondary succession is initiated when an existing plant cover is at least partially destroyed. Processes include burning, logging, flooding, grazing. Secondary succession is much more complex than primary succession due to variability in disturbance severity and spatial characteristics, seed bank characteristics and others.

Concepts of vegetation which provide a framework for development of successional models can be loosely grouped into two classes: individualistic and organismal. The organismal concept was first widely proposed by Clements (1916) and supported later by Odum (1969), Whittaker (1975) and Margalef (1968). It is based on the notion of autogenically-controlled succession in which the plants are co-adapted to their environment (i.e., adapt to and alter their environment). The community evolves as a super-organism resulting in greater homeostasis with the environment. Based on this concept, Odum and Whittaker support the monoclimax theory, which states that for a given prevailing climate, the community will tend toward one type.

The individualistic concept of vegetation succession was first proposed by Gleason (1926) and subsequently supported by Drury and Nisbet (1973), Salt (1979), and Glenn-Lewin (1980). In this model, the major process of succession is the replacement of one species by another in response to adaptation to the environment. The community is not a super-organism, rather it is the sum of its parts. This relates to the polyclimax theory (Tansley 1935) which considers the role of the environment (e.g., topography, moisture, drainage) in creating a mosaic of climax communities.

Tansley (1935) proposed a combination of the above. Collier et al. (1973) and Goodall (1966) do not regard these as exclusive concepts. Most present-day researchers subscribe to this intermediate view. The community is seen to have some control on the environment, and there are some groups of co-adapted species, but plants are mostly individualistic.

Connell and Slatyer (1977) have presented three models of plant succession based on life histories of initial and subsequent species. Facilitation: The later species become established and grow only after the earlier colonizing species have suitably altered the growing conditions (autogenic succession). Tolerance: The later species will be successfully established and grow to maturity even in the presence of earlier-established species. Their growth may be reduced, however, until the colonizers are in decline. Inhibition: The later species can grow to maturity only after the earlier species become absent.

Along with the substantial body of successional theory discussed above, models have also been developed which attempt to predict the changes which will occur in plant pattern during succession. Greig-Smith (1964) presented an elegant model which describes these changes. This model is discussed in detail in the body of the thesis, so will not be presented here. He admitted that it was based mostly on theoretical grounds and that field research was needed to verify it.

Of the many studies done on primary succession, only those from glacial and volcanic deposits can be considered as "true" primary succession (Heath 1967). This is because in succession on other deposits (e.g., mudflows, alluvium) there is often organic matter incorporated in the substrate. Establishment of plants on recently deglaciated terrain has been studied for at least 130 years in the European Alps and for about 60 years in North America and Scandinavia. The fact that plant succession in these environments begins on unaltered material helps to remove much of the "noise" (e.g, prior site history) associated with studies of secondary succession. The main value of studies of primary succession on deglaciated terrain is its contribution to development of succession theory (Elven 1980).

1.2 Research Objectives and Hypotheses

There were two objectives in this research:

(1) Determine the changes in pattern components (scale, intensity and patch/gap size) during primary succession on glacial moraines and outwash surfaces of known ages at two locations in the Canadian Rocky Mountains.

(2) Describe the process and determine the rate of plant community development during primary succession on proglacial moraines of known ages in the Canadian Rocky Mountains.

The general hypotheses tested were as follows:

1. Nucleation hypothesis

   Clones of *Dryas drummondii* act as centres of nucleation for subsequent recruitment of conifer and shrub species.

2. Pattern Hypothesis

The development of species pattern (scale, intensity, patch/gap size) during primary succession in proglacial environments follows the course outlined by Greig-Smith (1964). This development is repeated for both the colonizing (*Dryas drummondii*) and persistent (conifers, shrubs and non-vascular) species groups.

3. Plant Community Development Hypothesis

Primary plant succession (community development) on proglacial deposits proceeds in a unidirectional, predictable manner; floristically, structurally and in terms of diversity. The plant community characteristics vary most along the fourth dimension, which is time (as approximated by distance from the glacier).

Due to the two-fold nature of the research objectives in this thesis, the research is presented in two separate sections, with an introductory section containing material applicable to both.

1.3 Research Area

1.3.1 General Description

Two study sites were chosen for this research. They are located in the Main Ranges of the southern Canadian Rocky Mountains, in the Province of Alberta (Figure 1-1). The first site is on the proglacial moraine deposits adjacent to the Southeast Lyell and Mons Glaciers, which lie at the head of the Glacier River Valley (51° 54' N, 116° 58' W), 19 km WSW of Saskatchewan River Crossing, Banff National Park (Plates 1-1 and 1-2). The second site is located along the Icefield Parkway in the Columbia Icefield area, Jasper National Park (52° 13' N, 117° 14' W.). It encompasses the glaciofluvial outwash adjacent to the Dome Glacier and the outwash terraces along the Sunwapta River 1.5-3.0 km downstream from the Dome Glacier (Plates 1-3 and 1-4).

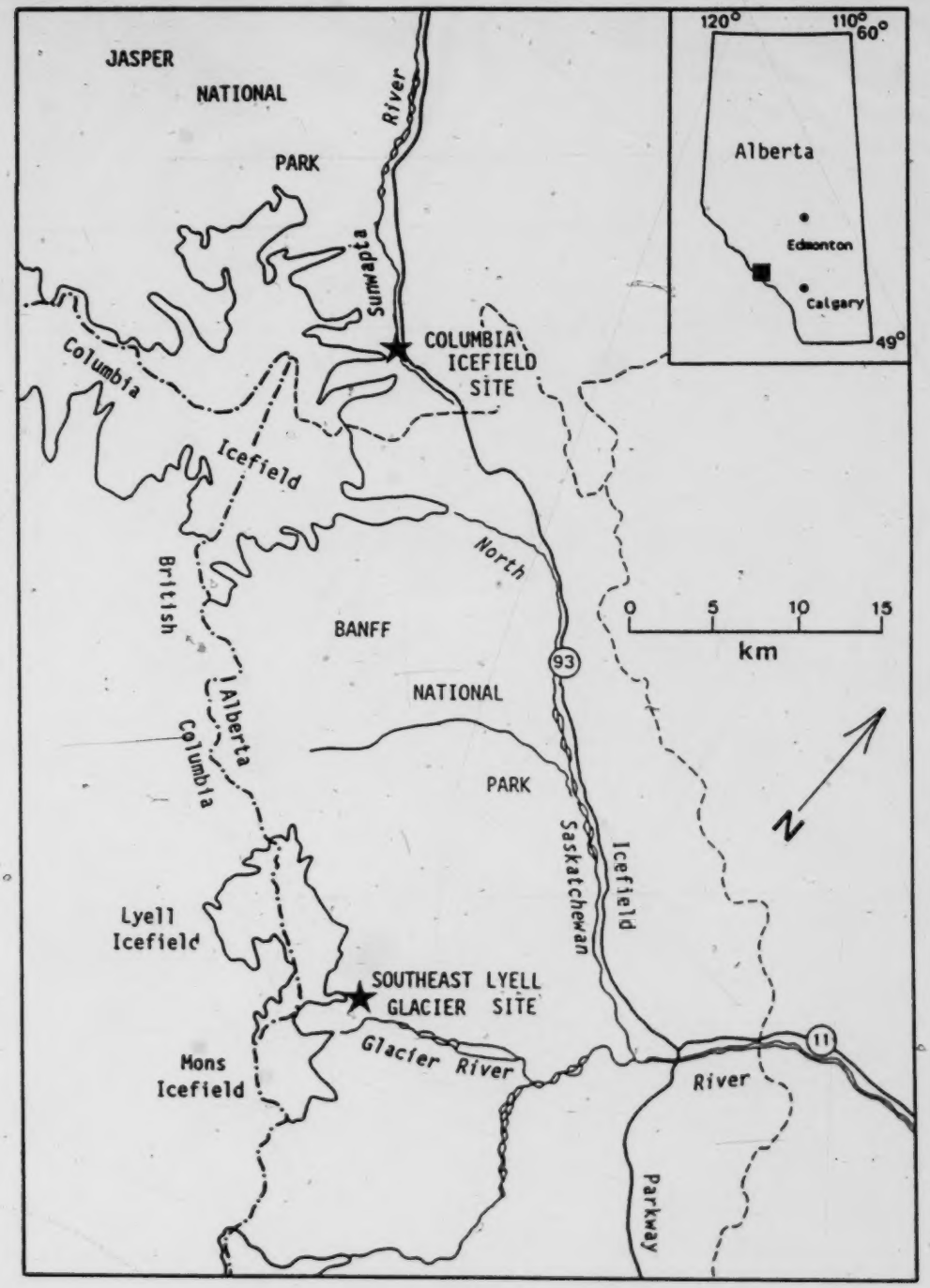

Figure 1-1 Study Site Locations

The reasons for choosing these two sites were as follows:

1. Accessibility:

   Highway 93 (The Icefield Parkway) runs adjacent to the Icefield study site so it is very accessible. While the Southeast Lyell Glacier site is 19 km from Highway 93, access was not a problem using pack horses.

2. Stable Surfaces of Different Ages:

   Often proglacial surfaces are continuously modified by glaciofluvial processes after glacial recession. Both these sites have a sequence of different age surfaces which became stable after deglaciation, thus allowing the uninterrupted development of vegetation on them.

3. Glacial Chronology:

   There is accurate information on the rate of glacial retreat, the position of the glacial termini in different years, and thus, the time at which portions of the proglacial deposits became stable. These information sources include casual observations, surveys and aerial photographs.

4. Contrasting Vegetation Chronosequences:

   The Southeast Lyell site has a well-developed primary vegetation chronosequence. A complete series of plant community development is represented ranging from open scattered *Dryas drummondii* communities to closed *Picea engelmannii* forest communities. In contrast, the open glaciofluvial deposits at the Icefield site represent a primary succession dominated throughout by *Dryas drummondii*.

1.3.1.1 Southeast Lyell Glacier Site

The Southeast Lyell Glacier study site comprises the upper portion of the Glacier River Valley, which until recent time, was covered by the Southeast Lyell and Mons Glaciers (Plate 1-1). The Southeast Lyell Glacier emanates from the southeast margin of the Lyell Icefield. This 50 km^2 icefield straddles the Alberta-British Columbia boundary for approximately 10 km between Division Mountain and the four peaks of Mount Lyell at an altitude of 2500 - 3450 m (Wheeler 1932). The Southeast Lyell Glacier is classified as a valley outlet glacier; 15.6 km^2 in area and 10.9 km in length, with a maximum and mean elevation of 3505 m and 2820 m, respectively (1952 measurements cited by Ommanney 1976, 1977).

Flowing southeastward for most of its length, in the last several kilometres, the tongue of ice curves northeast and eastward. At this point, it descends steeply to the valley floor down an icefall of 500 m, over the lip of a large amphitheatre (Plate 1-2). This icefall is one of the largest known in mid-latitude regions and exceeds any in the European Alps (Outram 1905). The snout rests at 1600 m at the base of this amphitheatre. Avalanches from the icefield above the valley headwall to the north feed more ice to the glacier terminus. The glacial runoff drains eastward into the Glacier River, in the upper North Saskatchewan River watershed.

The Mons Glacier is a second, much smaller glacier that flows into the main valley from the south via a small narrow SW-NE trending valley, two kilometres from the southeast Lyell Glacier. It is fed by the Mons Icefield (25 km^2 in area), and lies between Division Mountain and Messines Mountain (3136 m), mostly on the Alberta side of the interprovincial boundary. This glacier flows northeastward from the Mons Icefield, but only extends a little way into the valley proper, with its terminus resting at an altitude of 2020 m.

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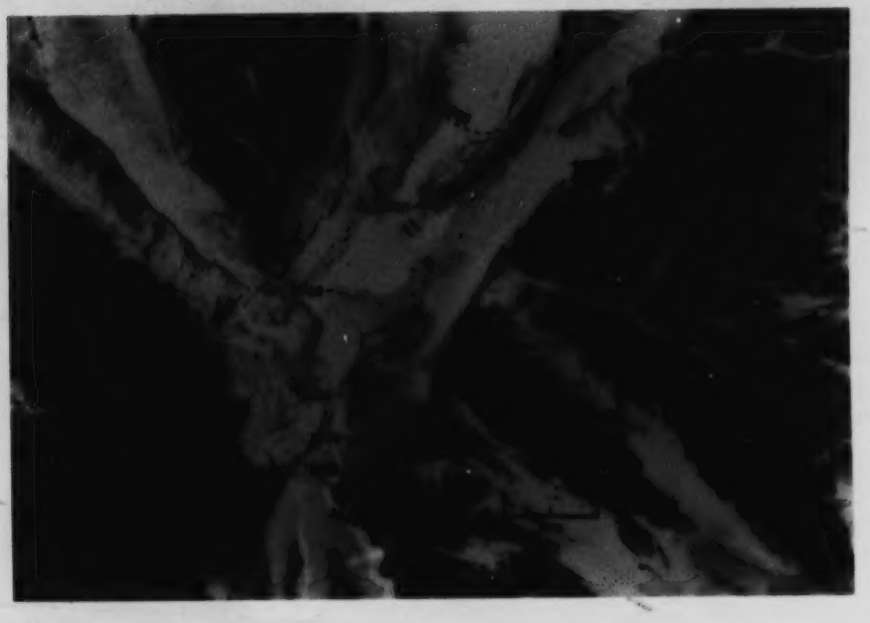

Plate 1-1 Aerial Photograph of Southeast Lyell Site
(August 1950 B&W Roll: A-12765 Photo 41 1:24,000)

Plate 1-2 Panoramic Photograph of Southeast Lyell Site from
Rock Promontory Near the Terminal Moraine. June 1984

1.3.1.2 Columbia Icefield Site

The Columbia Icefield, covering 230 km^2, is the largest icefield in the Rocky Mountains. It is situated on a broad high plateau along the Continental Divide at the southern end of Jasper National Park, Alberta, and adjacent parts of Banff National Park, Alberta and Hamber Provincial Park, British Columbia. Ringed by mountains from 3100 m to 3750 m in height, its ice lies at a mean altitude of 2900 m (Kucera 1972) and is from 100 m to 365 m thick (Harmon and Robinson 1981).

The Icefield feeds more than 30 glaciers, with the three largest (in descending order): the Saskatchewan to the east, the Athabasca to the northeast and the Columbia to the northwest (Denton 1975). Numerous other glaciers of several kinds emanate from the Icefield, including smaller valley glaciers, niche and hanging glaciers.

Both the Dome and Athabasca Glaciers are classified as outlet valley glaciers (Baranowski and Henoch 1978). The Dome Glacier is located just north of the Athabasca Glacier and is separated from it by a high rock spur. It is undernourished compared to the Athabasca Glacier, and over 35 percent of its surface is covered by ablation till and lateral and medial moraines, derived from rubble from rock avalanches plus rock carried within the glacier (Harmon and Robinson 1981). Including the accumulation area, the Dome Glacier is presently 5.5 km long. It flows in a northeast direction down a 750 m icefall with its terminus resting at 2000 m elevation.

Meltwaters from the Dome and Athabasca Glaciers empty into the Sunwapta River which flows northwest to join the Athabasca River, a major river in the MacKenzie River watershed.

Plate 1-3 Aerial Photograph of Columbia Icefield Site (August 1981 B&W Roll: A-25818 Photos 13 and 14 1:9,900)

Plate 1-4 Columbia Icefield Site from Icefield Parkway. Sunwapta Site in foreground, Dome Site in distance near forested slope. (Camera location near "B" on Plate 1-3). August 1984

1.3.2 Physiography and Geology

Jasper and Banff National Parks are found within the Southern Rocky Mountains which are part of the Rocky Mountain area in the Eastern System of the Cordilleran Region of Canada (Bostock 1970). Geologically, both study sites are situated within the eastern sector of the Main Ranges geological subprovince, in the southern portion of the Rocky Mountain Thrust Belt Sector (Douglas et al. 1970). This subprovince includes the Winston Churchill Range near the Columbia Icefield and the Lyell-Freshfield Mountain Group by the Southeast Lyell Glacier. The Main Ranges include most of the icefields and glaciers and almost all of the highest peaks in the Canadian Rockies, from Mount Assiniboine in the south to Mount Robson in the north. North of Simpson Pass it also almost continuously includes the Continental Divide.

Structurally, the Main Ranges are not as geologically complicated as, and are less disturbed than the Front Ranges, with substantially less folding (Baird 1977a). These mountains, which are composed mostly of thick sequences of distinctly bedded, horizontal or gently dipping resistant carbonates, quartzites, and minor shaly and slaty units, are more massive than the Front Range mountains (Price and Mountjoy 1970). The sedimentary rock which comprise the Main ranges have been greatly uplifted, with erosion having stripped off the younger rocks to expose older rocks at the surface (Baird 1977b). These rocks, mainly of Precambrian and Lower Paleozoic sediments, are among the oldest found in this area of the Rocky Mountain System (Balley et al. 1966). The headwaters of the North Saskatchewan and Sunwapta River systems are cut into these very old rocks with patches of younger rocks lying in the downfolds and preserved in the higher mountain peaks (Baird 1977b).

1.3.2.1 Southeast Lyell Glacier Site

The Glacier River is contained within an east-west aligned canyon valley. Steep-sided valley walls rise more than 1000 m on both sides,

providing good geological exposure. In the immediate vicinity of the Southeast Lyell Glacier the evenly bedded rock strata dip to the southwest of an angle of 10 to 20° (Walcott 1920).

The geological stratigraphy of the Glacier River Valley has been described in detail by C.D. Walcott (1920, 1923, 1928) and more recently by Aitken and Greggs (1967) and Aitken and Norford (1967). It consists of thick sequences of mostly carbonate rocks, ranging in age from Upper Cambrian to Devonian (Wheeler et al. 1972). Younger Rundle Formation limestone rocks of Mississippian age are preserved in the peaks of the higher mountains (Forbes, Outram, Mons) which border the south margin of the valley (Walcott 1928, Hughes 1955).

At the valley headwall between the Mons and Southeast Lyell Glacier, the Upper Cambrian strata are embodied in three depositional cycles: Arctomys-Waterfowl, Sullivan-Lyell, Bison Creek-Mistaya (Aitken and Greggs 1967). The lower formation of each cycle is composed mostly of shales grading into limestones in the upper formation (Table 1-1).

The Upper Cambrian Arctomys, Waterfowl and Sullivan Formations outcrop along the valley walls downstream from the terminal (end) moraine. A large rock promontory on the south side of the Glacier River across from the terminal moraine is composed of limestone of the Upper Cambrian Formation. Proceeding upslope from that point, a complete sequence of Upper Cambrian to Upper Devonian rocks are exposed, culminating with limestones of the Upper Devonian Palliser Formation at the summit of Division Mountain, on the Continental Divide. This sequence is more than 2000 m thick and is summarized in Table 1-1.

The Lyell and Mons Icefields are underlain by Upper Devonian and Ordovician limestones and dolomites (Aitken and Greggs 1967). The large cliff walls over which the Southeast Lyell Glacier tumbles are composed of Ordovician rock. A massive limestone member of the Survey Peak Formation caps the headwall; below that, calcareous shale of the same

TABLE 1-1

GEOLOGICAL STRATIGRAPHIC COLUMN

VALLEY HEADWALL AT THE SOUTHEAST LYELL GLACIER

Age	Formation	Thickness (m)	Lithology
Upper Devonian	Palliser Formation	?	Upper Member: Moderately resistant dark grey thin-bedded limestone. Lower Member: Cliff-forming pale grey thick-bedded limestone.
Upper Devonian	Fairholme Group (undivided)	62 +	Cliff-forming dark grey sandy thick-bedded massive dolomite; bands of near-white medium-bedded quartzite; minor limestone, shale and mudstone bands at top.
Upper Devonian	Owen Creek Formation	225	Light to dark grey dense thick-bedded massive dolomite; minor dolomitic and quartzose sandstone.
Middle Ordovician	Skoki Formation	103	Resistant dark grey to grey massive dolomite.
Lower Ordovician	Outram Formation	442	Grey medium to thick-bedded limestone, often clotted or nodulated in a matrix of dark grey slaty slightly calcareous shale; calcareous quartzose siltstone; minor dolomite.
Lower Ordovician	Survey Peak Formation	477	Upper Massive Member: Cliff-forming thick-bedded massive limestone and limestone-pebble conglomerates; black chert; minor shale. Putty Shale Member: Recessive olive to olive-grey calcareous shale; some limestone. Basal Silty Member: Grey calcareous shale; silty calcisiltite and calcareous siltstone.
Upper Cambrian	Mistaya Formation	160	Resistant grey massive thrombolitic limestone; some biocalcarenite.
Upper Cambrian	Bison Creek Formation	200	Calcareous shale; bands of dark bluish-grey limestone.
Upper Cambrian	Lyell Formation	518	Dark and medium grey to bluish-grey massive limestone.
Total Thickness		2187 +	

Based on Aitken and Norford 1967, with additions by Walcott 1928, Wheeler 1962 and Ollerenshaw and Hills 1978.

formation is exposed along the cliff face. The less steep rock slopes near the snout of the glacier are calcareous shales and limestones of the Upper Cambrian Mistaya, Bison Creek and Lyell Formations.

In summary, the parent material for the glacial debris within the study site is mostly a mixture of calcareous shale, limestone and dolomite, with some quartzose siltstone and sandstone.

1.3.2.2 Columbia Icefield Site

Compared to the detailed stratigraphic information available for the Southeast Lyell site, there is not much geological information for the immediate vicinity of Dome Glacier and the Sunwapta River glaciofluvial outwash. Most of the literature on the area is centred around Nigel Peak and Sunwapta Pass six to eight km to the east (e.g., Allan 1938, Severson 1950, Ollerenshaw and Hills 1978).

The mountains which border the northeastern flank of the Columbia Icefield from which flow the Dome and Athabasca Glaciers are formed from Middle Cambrian massive carbonate rock (Wheeler et al. 1972). These mountains (Kitchener, Andromeda and Athabasca) are composed mainly of limestone with lesser amounts of shale and quartzite (Kucera 1972). They are susceptible to frost shattering, because of their numerous fractures, resulting in large amounts of rock debris, such as that found along the lower stretches of the Dome Glacier.

Low on the northeast shoulder of Mount Athabasca, rocks of Upper Cambrian and Lower Ordovician age are exposed, including dolomite, shale limestone (International Geological Congress 1972a) (Table 1-2). These rocks are separated from rocks of Middle Cambrian age which form the main mass of Mount Athabasca and adjacent mountains by the Simpson Pass thrust fault. Above this fault, near the exposed base of Mounts Athabasca, Andromeda and Kitchener are resistant dolomites of the Cathedral Formation. Recessive shales, capped by resistant dolomites and

TABLE 1-2

GENERALIZED GEOLOGICAL STRATIGRAPHIC COLUMN

DONE GLACIER - SUNWAPTA PASS

(Top of Nigel Peak to Sunwapta River Valley Bottom)

Age	Formation	Thickness (m)	Lithology
Mississippian	Rundle	90	Cliff-forming massive, resistant grey to black limestone, and dolomitic limestones; some shale bands.
Mississippian	Banff	490	Grey and brown calcareous shales with interbedded limestone.
Devonian	Exshaw	50	Upper Member: Massive grey and brown limestone. Lower Member: Black, non-calcareous shale.
Devonian	Palliser	580	Major cliff-forming unit. Massive light to dark grey limestone; black chert nodules in top.
Devonian	Fairholme	410	Dark grey to black limestone; sandy near base.
Lower Ordovician	Survey Peak	580	Massive, white, well cemented sandstone; dark grey to black cherty limestones; greenish-grey shales.
Upper Cambrian	Mistaya	↑	Resistant grey massive limestones.
Upper Cambrian	Bison Creek		Calcarious shale.
Upper Cambrian	Lyell		Massive dark and medium grey limestone.
Middle Cambrian	Arctomys	760 +	Red and green shales; dolomitic sandstones at base.
Middle Cambrian	Pika	↓	Resistant dolomites and limestones.
Middle Cambrian	Eldon		Cliff-forming resistant massive dark grey to black dolomite.
Middle Cambrian	Stephen		Recessive shales; some limestone.
Middle Cambrian	Cathedral		Cliff-forming resistant massive grey limestones and dolomites with sandy and shaly sections.
Total Thickness		2960 +	

Based on Baird 1977b, Severson 1950, Hughes 1955, International Geological Congress 1972a.

limestones of the Eldon and Pika Formation comprise much of the valley headwall over which flows the Dome Glacier (International Geological Congress 1972a, 1972b). In the valley bottom, near the Parks Canada Information Centre, across from the terminus of the Athabasca Glacier are outcrops of red and green shales and orange dolomitic siltstones of the Middle Cambrian Arctomys Formation (Wheeler et al. 1972).

In comparison to the rocks just described, the strata exposed on the northeast side of the upper Sunwapta River valley are younger, ranging in age from Upper Cambrian on the lower slopes to Mississippian along the Tangle Ridge Syncline at the crest of the Nigel Peak. The strata on this side of the valley near Wilcox Peak are more massive and contain more limestone than the rocks exposed across the valley on Mount Kitchener, which are more shaly (Allan 1938).

Along the bottom of the Sunwapta River valley, near the study sites, the strata dips 10° to 45° (Alberta Society of Petroleum Geologists 1955). To the west near the anticline axis by Mount Kitchener, the sedimentary strata are nearly horizontal (Baird 1977b).

In summary, the glaciofluvial outwash at the Columbia Icefield site is comprised mostly of limestone, dolomite, shale and quartzite (in decreasing order of importance) (Welch 1967).

1.3.3 Regional and Local Climate

The climate of the Canadian Rocky Mountains is variable, with large fluctuations in conditions on a yearly, seasonal, daily and even hourly basis (Ogilvie 1976, Janz and Storr 1977). Due to its distance from the Pacific Ocean and the northwest-southeast trending orientation of the main mountain ranges (which are almost at right angles to the prevailing southwest winds) the air masses which flow over the mountain parks are usually dry, resulting in a continental climate relative to coastal

mountain areas (Holland et al. 1982). There is some oceanic influence, however, especially along the Continental Divide, and this, combined with high elevations and northerly latitude results in a rather cool and moist climate in the study region (Ogilvie 1976).

According to Koeppen's climate classification, the study area has a Dfc climate. Summers are cool, showery and frost-prone, while the winters are cold with abundant snowfall (Ecoregions Working Group 1989). The climate is further characterized by a short plant growth season of 70 to 100 days per year, and a low rate of evapotranspiration (Kojima 1980).

1.3.3.1 Southeast Lyell Glacier Site

The Southeast Lyell Glacier site lies within the southern Cordillera Subalpine ecoclimate region as defined by the Ecoregions Working Group (1989). Due to its relatively low elevation, it is within the Lower Subalpine ecoregion. Downvalley, a montane ecoclimate exists along the North Saskatchewan River Valley. These relatively dry and mild conditions extend upvalley as far as the east end of Glacier Lake, nine km from the study site (Strong and Leggat 1981). The influence of these warmer, drier conditions can be found at the study site. *Pseudotsuga menziesii*, which is a montane climate indicator species (Janz and Storr 1977), grows on some of the older moraine surfaces near the terminal moraine. Several factors, as well as a low elevation, probably contribute to its presence. The surfaces on which it grows slope gently to the south and southwest, which greatly increase the radiation received (Janz and Storr 1977). The high mountains on the south side of the valley are set back so the valley bottom is not often in shadow. A survey of the horizon height was taken at the meteorological field station established during the field research near transect 6a (Figure 2-4). From 90° to 270° azimuth, the horizon angle averages 18.7° with the highest peaks at an angle of only 21.5° to 29°.

Several other factors affect the climate at the Southeast Lyell site: close proximity to glaciers and icefields, presence of high mountains in the vicinity, and an east-west trending valley. The first two factors offset the effect of low elevation by contributing to a cooler and moister climate, while the third factor may contribute to higher wind speeds.

There are no climate stations in the immediate vicinity. The nearest station is at the Parks Canada wardens office at Saskatchewan River Crossing, 20 km ENE of the study site (Figure 1-1), where unpublished precipitation data are collected during the summer months. The climate is probably best represented by the data from Lake Louise, Alberta, 75 km to the southeast (Table 1-3), because both locations are near high mountains on the east side of the Continental Divide and at a similar altitude.

The climate at Lake Louise is cool and moist, and is representative of the subalpine ecoclimate in that region (Figure 1-2) (Ecoclimate Working Group 1989). The mean monthly temperature fluctuates from 12.2°C in July to -15.2°C in January, with a mean annual temperature of -0.4°C (Table 1-3) (Atmospheric Environment Service 1982a). During winter, Pacific air masses often result in milder conditions (Janz and Storr 1977).

At both study sites there is a general cool summer climate due to the proximity of ice masses. Studies have shown that katabatic winds can cool adjacent sites up to 4.7°C (Rannie 1977) and is most pronounced on hot sunny days. Studies at Peyto Glacier in Banff National Park indicate that the temperatures near the terminus are lowered by 2°C to 3°C for daytime highs and 1°C to 2°C for nighttime lows (Janz and Storr 1977). The downvalley cooling effect does not extend more than 1.5 km downvalley for most glaciers (Rannie 1977), and this is probably the case at the Southeast Lyell site.

TABLE 1-3

CLIMATE SUMMARY

FOR SOUTHEAST LYELL GLACIER AND COLUMBIA ICEFIELD SITES [1]

Climatic Parameters	Lake Louise Station (75 km SE of Southeast Lyell Glacier)	Columbia Icefield Station (5 km east of Dome/Sunwapta)
Location	51° 25'N 116° 10'W	52° 14'N 117° 10'W
Elevation	1524 m	1981 m
Ecoclimatic Region	Lower Subalpine	Upper Subalpine/Alpine
Observation Period	1951 - 1980	1961 - 1977(intermittent)
Mean Annual Temperature	-0.4° C	-2.1° C
Mean Daily Max. Temperature (July)	21.0° C	15.2° C
Mean Daily Min. Temperature (Jan)	-22.0° C	-19.0° C
Warmest Recorded Temperature	34.4° C	26.1° C
Coldest Recorded Temperature	-52.8° C	-41.1° C
Temperature Range of Yearly Mean Monthly values	43.0° C	34.2° C
Temperature Range of Extreme Values	87.2° C	67.2° C
2 Growing Degree Days Above 5° C	712	386
2 Thawing Degree Days Above 0° C	1552	1003
Mean Annual Precipitation	684mm	930mm
Number of Days With Precipitation	130	157
Percentage of Yearly Precipitation as Snow	61%	74%

Sources: Atmospheric Environment Service 1982a
Atmospheric Environment Service 1982b

1 The Southeast Lyell climatic data is represented by the Lake Louise Station.

2 Degree-Days (per day) = $\frac{\text{(maximum + minimum daily temperature)}}{2}$ − Reference Temperature

To get total degree-days for a year, the daily degree-days are summed.
A reference temperature of 5° C is used for growing degree-days.

During the 1984 field season, meteorological data was collected at two locations: 1) open area 1.3 km from glacier terminus 2) treed area 100 m inside the terminal moraine (1.9 km from the glacier terminus). In July of that year, the average maximum daily temperature was 21.7°C at both sites while the minimum was 5.6°C and 5.2°C at the two locations respectively. The overall mean temperature of the two sites combined was 13.6°C. The average July temperature at Lake Louise for that year was 12.5°C (1951-1980 average is 12.2°C) (Atmospheric Environment Service 1985). This means that the Southeast Lyell site may be slightly warmer than Lake Louise in summer (which helps explain the presence of *Pseudotsuga menziesii*).

Frost is possible during every month of the year in the subalpine. Over the period from 1941 to 1970, there was an average of 17 frost-free days every summer at Lake Louise, although this fluctuated widely each year from a low of 0 to a high of 67 days, based on data since 1915 (Janz and Storr 1977). In spite of local cooling by glaciers, sites near glaciers have a lower number of frosts during the summer months due to local stirring of air by off-glacier winds at night (Janz and Storr 1977).

The length of the frost-free period increased from the early 1950's to the 1970's (Janz and Storr 1977). As well, the annual number of summer days with frost (Junel-Aug 31), based on decade averages, has declined steadily from 39 in the 1920's to 17 in the 1970's (Janz and Storr 1977). Gardner (1968) studied mountain temperatures in the Lake Louise area and found that they have been increasing since the late 1950's.

Both the study sites lie in a zone of heavy precipitation which runs along the Continental Divide from Athabasca Pass to Freshfield Icefield (Janz and Storr 1977). At the Lake Louise station there is a well--defined winter maximum of 97.9 mm in December. Spring and autumn are drier with a weak secondary maximum of 57.5 mm in June (Figure 1-2).

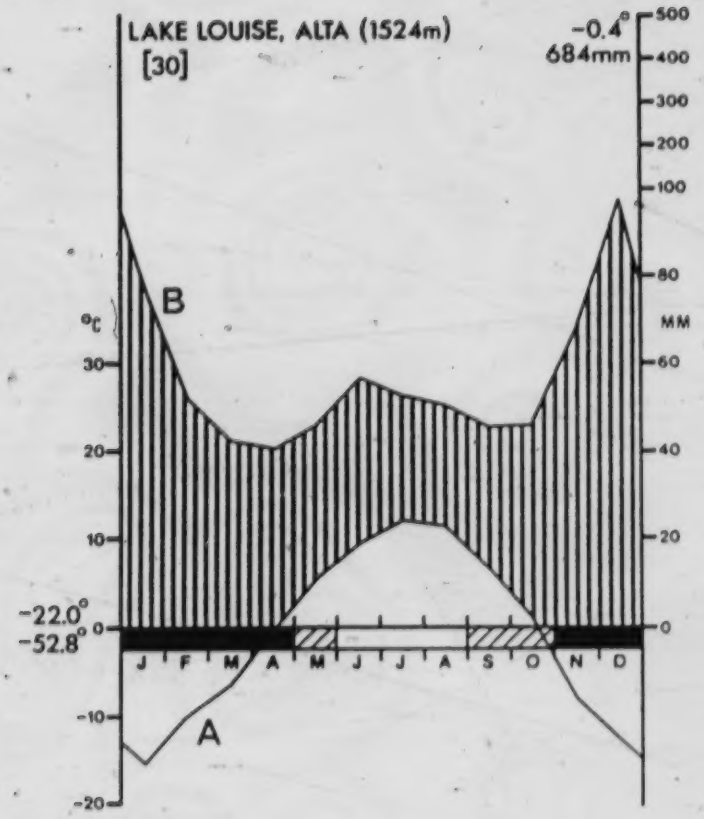

Figure 1-2 Climate Diagram - Lake Louise, Alberta

Legend

A - Curve of mean monthly temperature (0°C)
B - Curve of mean monthly precipitation (mm)

Solid Black - Months with mean daily temperatures below 0°C.
Diagonal Pattern - Months with mean daily temperatures above 0°C. but mean daily minimum temperatures below 0°C.
Vertical Pattern - Period of relatively humid climate.

Based on 30 year data from 1951 to 1980 (see Appendix 1-1A).

Modified from Ecoregion Working Group (1989).

Total precipitation at the Southeast Lyell site is probably a little higher than at Lake Louise. On a precipitation map by Janz and Storr it is estimated at 750 - 1000 mm (compared to 684 mm at Lake Louise).

Snow distribution was measured at the study site during a reconnaissance trip in late February 1985. The snowpack was deeper and less windblown at the study site than further downvalley, although conditions varied greatly. In the more sheltered locations near the terminal moraine, the snowpack was quite deep, ranging from 71 cm to 95 cm (mean = 80 cm), with snow evenly distributed on moraines and in hollows. On slightly more exposed locations, upvalley from the terminal moraine, large moraines had between 50 and 70 cm of snow on their lower slopes with between 0 and 15 cm of snow on the exposed crests. Leeward slope snowdrifts were thick, over 130 cm deep in places. Closer to the glacier, the snow was quite windblown. On the gently sloping ground moraine near the glacier snout, the snow ranged in depths from 38 cm to 99 cm (mean= 52 cm); the only surfaces bare of snow were along some moraine crests and rock outcrops. It is not known if these conditions were typical for the site.

At upper levels, winds are usually from west to southwest; at the surface, topography determines prevailing wind direction (Janz and Storr 1977). Because of the orientation of the major valleys, prevailing winds in the Glacier Lake area are from the southwest, based on data from the Saskatchewan River Crossing (Janz and Storr 1977). This is comparable to data from the Bighorn Dam station, further downvalley, where winds blow from the southwest almost 40 percent of the time (Atmospheric Environment Service 1982c). These are funnelled along the west-east trending valleys, causing strong chinook winds downvalley from Glacier Lake (Janz and Storr 1977), however, these winds are not common upvalley in the subalpine zone near the study site (Holland et al. 1982).

Katabatic winds flowing off ice bodies can create locally windier areas around glacial termini (Janz and Storr 1977). This condition was

noticed during the 1984 field season and is confirmed by the effect of strong winds on *Picea* and *Abies* saplings near the glacier which are strongly flagged with brown and desiccated needles. Strong winds blow down the centre of the valley resulting in a lag in vegetation development on the moraines south of the Glacier River. North of the river, where the thesis research was conducted, winds are less severe, perhaps due in part to the protection by the large trees growing there. It may also be because the strongest glacier winds flow down the valley centre, with little lateral movement (Janz and Storr 1977).

In summary, the climate at the Southeast Lyell Glacier site is comparable to that at Lake Louise, although at the former location there is some local effect due to the glacier. As well, winters are probably more snowy and summers slightly warmer than at Lake Louise.

1.3.3.2 Columbia Icefield Site

The climate near the Columbia Icefield is transitional between subalpine and alpine. The actual study site is located within the upper subalpine. Major physiographic factors include its high elevation (1910 m above sea level) and close proximity to the Columbia Icefield. Because of its exposed location, and the fact that it is 420 m higher than the Southeast Lyell site, the climate at the Icefield study site is more maritime in character, with cooler, cloudier, wetter and more windy conditions (Janz and Storr 1977).

The Columbia Icefield Station, located five km east of the study area in the subalpine/alpine transition zone, has climatological records dating back to 1961, and a comprehensive data summary has been published by the Atmospheric Environment Service (1982a). Figure 1-3 is the climate summary diagram for this station.

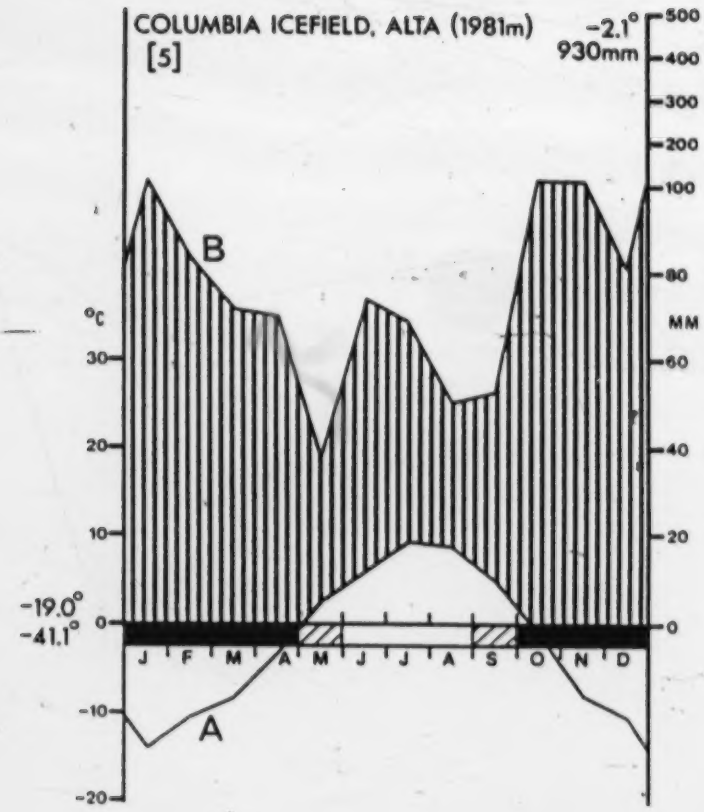

Figure 1-3 Climate Diagram - Columbia Icefield, Alberta

Legend

A - Curve of mean monthly temperature (0°C)
B - Curve of mean monthly precipitation (mm)

Solid Black - Months with mean daily temperatures below 0°C.
Diagonal Pattern - Months with mean daily temperatures above 0°C. but mean daily minimum temperatures below 0°C.
Vertical Pattern - Period of relatively humid climate.

Modified from Ecoregion Working Group (1989).

Compared to the lower elevation study area, the mean annual temperature of -2.1°C is 1.4°C colder (Table 1-3). This cooler climate is reflected in the low number of growing degree-days above 5°C which are half as many as at the Lake Louise station (Table 1-3). The period of average daily temperatures above freezing is about five months, one month shorter than at Lake Louise (Figures 1-2 and 1-3). Compared to the lower subalpine zone, summer temperatures at the Icefield are cooler (July mean is 9.1°C) and the winter temperatures are warmer (January mean is -14.2°C) which is a common situation in higher elevations in the Canadian Rockies (Strong and Leggat 1981). The milder winter temperatures at higher elevations are due to the common occurrence of temperature inversions in the mountain valleys (Holland et al. 1982).

The Columbia Icefield exerts a greater cooling influence on the climate of the Dome/Sunwapta site than is the case at the Southeast Lyell Glacier, probably for three reasons: 1) The Columbia Icefield is 230 km^2 in area while the Lyell and Mons Icefields have a total combined area of only 75 km^2. 2) The general altitude of the Columbia Icefield is higher. 3) Off-glacier winds from the Lyell Icefield drop at least 1500 m before reaching the proglacial deposits while at the Columbia Icefield, there is a drop of only about 1000 m to the upper Sunwapta River. In the latter case, there is less chance for the descending air to warm adiabatically.

In the mountains, the occurrence of non-winter frosts is increased by proximity to glaciers, high elevation and open areas (which allow cold air to move in) (Janz and Storr 1977). The Dome/Sunwapta site has all these characteristics. However, as discussed earlier, off-glacier winds can mix the lower air layers, resulting in fewer days with frost during the summer at the Columbia Icefield than at lower elevation sites such as Lake Louise. Frosts are most frequent during spring and autumn. For example, in June 1966, Welch (1967) found that freeze-thaw cycles occurred every day. Because of the high altitude, frosts are probably more frequent here during these seasons compared to lower altitude

locations. The presence of extensive areas of needle-ice on the finer-textured materials attest to the strong frost action in the vicinity.

The total annual precipitation at the Columbia Icefield is higher than at Lake Louise (Table 1-3), although the distribution of precipitation throughout the year is similar (Figures 1-2 and 1-3). Late fall and winter are the times of greatest precipitation. There is also a pronounced smaller peak in precipitation in June and July, partly due, perhaps to increased convective precipitation. The average of 157 days of precipitation during the year (Atmospheric Environment Service 1982a) is the highest of any station in the mountain parks (Janz and Storr 1977). This high frequency is probably due to the high elevation and large total annual precipitation.

There is higher snowfall at the Icefield site than at the Southeast Lyell site, with 74 percent of the precipitation in the form of snow (Atmospheric Environment Service 1982a). Strong winds rework the snow, so that on the exposed glaciofluvial deposits, the snow is hard packed and relatively shallow. During the late February 1985 reconnaissance trip, measurements indicated depths of 13 cm to 30 cm of snow on the exposed flats. In some of the shallow abandoned river channels snowdrifts were up to 50 cm deep. The upright leaves and old scapes of *Dryas drummondii* clones trap the snow, so wherever it occurs snow depth is at least 10 cm. Exposed bare ground is found on the crests of some of the moraines by the Dome Glacier and on the upper edge of some of the terrace risers. Snowdrift patterns indicate that at the Dome Glacier, the prevailing winter winds are from the southwest off of the glacier, while along the Sunwapta River, the major winds flow up the valley from the northwest.

Winds in the vicinity can be high, especially in winter, partly due to the higher altitude (Ogilvie 1976). Since the strength and effects of glacier wind depend on the size and orientation of the ice body, the katabatic wind-flow off the Columbia Icefield is strong (Janz and Storr

1977). Both the katabatic winds and the regional air flow are channelled up and down the upper Sunwapta River Valley, so that the dominant wind directions are from the southeast and northwest (Janz and Storr 1977). This means that the proglacial deposits by the study site are quite exposed. The effects of strong winds were seen during the 1984 field season through deflation of fine particles on exposed bare ground, extreme flagging of conifer saplings and flipping over the edges of *Dryas drummondii* clones.

In summary, the climate at the Columbia Icefield is cooler, wetter and windier than the climate at the Southeast Lyell Glacier. This no doubt influences the path of successional development as described later.

1.3.4 Glacial Chronology

The glacial history of the central Canadian Rocky Mountains since the late Wisconsin glacial period has been well documented in recent years (see Luckman and Osborn 1979). There are still disputes, however, as to some of the details (e.g., Harris and Howell 1977, Luckman et al. 1978). In spite of this, the general history can be outlined.

Direct methods (photographs, observations or surveys taken over a period of time) or indirect methods such as dendrochronology, lichenometry, tephronology (volcanic ash analysis) and radiocarbon dating can be used to date glacial deposits in the central Canadian Rocky Mountains (Luckman and Osborn 1979). In the latter group, dendrochronology is one of the most widely used methods for dating glacial deposits below treeline. Discussions of dendrochronological methods can be found in Lawrence (1950), Heusser (1956), Palmer and Miller (1961), Viereck (1968), Sigafoos and Hendricks (1969) and Shroder (1980).

Heusser (1956) and Viereck (1968) have tried to determine the average number of years between deglaciation and establishment of seedlings in order to estimate more accurately the time of deglaciation using growth-ring analysis. This time interval is a function of microsite and surface stability conditions, climate and seed source. In western North America it varies from five years in Washington State to near 100 years at some sub-arctic sites in Alaska (Viereck 1968). In the Canadian Rocky Mountains it varies from 10 to 30 years (Heusser 1956). This method is best used when there is photographic evidence to determine the interval period accurately.

Much additional dendrochronological information can be gleaned from shrubs, especially where conifer saplings are only sparsely distributed, such as at the Columbia Icefield site. Often, in the upper subalpine climate, shrubs are established long before the conifers (see Appendices 1-2B and 1-2C). Unfortunately, previous researchers in the area restricted their sampling to coniferous tree species.

In areas close to the Continental Divide and near existing glaciers, deglaciation after the Late-Wisconsin advance occurred around 10,000 years before present (Luckman and Osborn 1979). At that time, the Late Wisconsin valley glaciers had receded to positions close to, or within present glacial limits. Since this deglaciation there have subsequently been two advances; both were quite limited in extent (Luckman and Osborn 1979). The first is called the Crowfoot Advance, and is represented by moraines and rock glaciers overlain by Mazama ash (6,600 years before present) and is therefore late Wisconsin or early Holocene in age.

The second advance is called the Cavell advance by Luckman and Osborn (1979) and occurred within the last few centuries. Compared to the Wisconsin age glaciation, both advances were limited in extent (only one or two km further than present glacier limits) and the latter usually overrode the former one. At the Athabasca Glacier, however,

Crowfoot Advance deposits occur about 0.5 km east (downslope) of the maximum Cavell Advance deposits (Luckman and Osborn 1979).

The Cavell Advance is correlated with the last several centuries of a cooler period called the "little ice age" by some authors and the "Neoglaciation" by others (Porter and Denton 1967). The latter term is more appropriate as this was a period of glacier expansion subsequent to a time of quite warm conditions from 7000 to 3500 years before present called the Hypsithermal (Heusser 1956). This neoglacial period lasted for at least 500 years, beginning in the 14th century and ending in the late 1800's (Luckman and Osborn 1979). These conditions resulted in a period of glacial advances in both the northern and southern hemisphere (Field 1949).

In the Canadian Rocky Mountains the earliest advances occurred from about 1350 to 1650 (Heusser 1956) while the date of maximum advance ranged from the early 17th century to the latter part of the 19th century (Field 1949). The glaciers in temperate North America registered four prominent maxima within this time, although these maxima did not occur at each location (Heusser 1956). Since the mid to late 1800's, almost all of the glaciers in the Rocky Mountain Region continuously retreated (Meek 1948), although it has not taken place at a constant rate, nor has it been uniform between glaciers (Gardner 1972).

Attempts to correlate glacier activity with the climate of the time can be quite difficult because the linkages between the past and present climates and glacier activity are quite complex (Ommanney 1976). The time required for glacier activity to respond to a change in climate can vary, ranging from perhaps a few years for a small niche glacier to around 100 years for the Athabasca Glacier which is fed by a large icefield (Ommanney 1976). Physical terrain factors also play a major role in glacier activity. The temporary presence of terminal lakes such as at the Athabasca and Southeast Lyell Glaciers has increased the rate of glacier withdrawal, while the ablation till which covers the Dome

Glacier terminus has acted as an insulator so that the tongue is almost stagnant and little recession has occurred recently (Heusser 1956).

The relationship between glacier activity and climate in the study region can be examined through records going back 100 years. The overall behaviour closely parallels meteorological trends at Banff and Lake Louise, with a lag time of about 20 years (Porter and Denton 1967).

Based on 10 year moving means, there was a general warming trend with drier conditions from the 1880's to the late 1930's (Porter and Denton 1967, Henock 1971). The 1940's and 1950's had an increase in precipitation and a decline in mean annual temperature. Since about 1960, conditions have again become warmer and drier (Gardner 1972, Water Survey of Canada 1982). During the latter half of the 19th century until about 1920, glaciers in the region retreated slowly and regularly, but the rate increased markedly thereafter, up until the early 1950's (Porter and Denton 1967, Gardner 1972). Beginning in the late 1950's the rate of recession for most glaciers started to slow down; this has become most pronounced in the past 15 years (Gardner 1972, Water Survey of Canada 1982). At present, the glaciers are still retreating slowly, even though the past 25 years have been warmer and drier. It may be that the glacier termini are almost in equilibrium with the generally warmer conditions and will not retreat much further over the next while.

Even with the recent slow down, total glacier recession in the past 60 years in this part of the Rocky Mountains has been rapid. Henock (1971) estimated that during the period between 1948 and 1966, the area covered by glaciers in the upper North Saskatchewan River basin decreased approximately 10 percent.

1.3.4.1 Southeast Lyell Glacier Chronology

The glacial history of the Southeast Lyell Glacier during the past 100 years is one of the best known in the Canadian Rockies. Observations

date back to 1858, when Dr. James Hector of the Palliser Expedition first visited the site. At that time he made the first detailed description of a glacier in the Canadian Rocky Mountains, which was published in 1860 (Thorington 1927b). Since then, numerous climbing parties have taken photographs and conducted surveys of the fluctuation of the glacial terminus.

In 1947 the glacier was surveyed as part of the Canadian Government monitoring program of glaciers in Banff and Jasper National Parks (McFarlane 1947). This was the only federal survey of this glacier, as it was decided that the glacier had receded too far, and the remainder was too steep for further surveys. In 1984, at my request, C.S. Ommanney of the National Hydrological Research Institute produced a document which lists most of the information available on the Southeast Lyell and Mons Glaciers (Ommanney 1984). Major articles cited in that publication, plus other ones that were uncovered during the thesis research, are listed in Table 1-4. Some of these surveys were quite thorough. They included the surveys by J.M. Thorington (1927a, 1927b, 1931a, 1931b) earlier in the century and the detailed work conducted by a party of the American Geographical Society in 1953 (Field 1979). The latter group took photographs from reference spots, where earlier photographs had been taken. Since July 1947, the study site has been recorded on aerial photography every few years (Appendix 1-1A). During the 1953 field season with the American Geographical Society, Calvin Heusser extracted 55 tree cores from the Southeast Lyell Glacier moraines in order to develop and confirm the glacial chronology for the site (Heusser 1956).

During the 1984 field season, material was collected to verify the previously published information. Approximately 225 tree cores and 180 root cores and stem disks of shrubs and small trees were taken. Appendix 1-2A and Table 1-5 give a summary of information for the oldest specimens collected along each transect. Based on extensive field studies during 1953, Heusser (1956) was able to determine the average time interval required after deglaciation for conifer seedlings to

TABLE 1-4

INFORMATION SOURCES FOR THE SOUTHEAST LYELL AND MONS GLACIERS CHRONOLOGY [1]

Date of Survey	Author, Publication Date	Type of Information	General Comments
1858	Hector 1860	detailed description and rough survey	Mons and SE Lyell Glaciers coalesced
1902	Outram 1904	brief description	Glaciers still coalesced
1918	Interprovincial Boundary Commission 1925	glaciers mapped (Sheet No. 19 at 1:62,500) and photographed	Mons Glacier has separated from SE Lyell Glacier
1919	Walcott 1920 Walcott 1928	description and panoramic photographs	
1926	Thorington 1927a Thorington 1927b	description, survey and photographs	SE Lyell snout eroded by Mons Glacier meltwater, causing rapid retreat
1930	Thorington 1931a Thorington 1931b	description, survey, maps and photographs	
1940	Kothe 1940	photographs	
1944	Thorington 1945a Thorington 1945b	description and survey	SE Lyell terminus lies in tarn, period of rapid retreat
1947	McFarlane 1947	survey and photographs	
1953	Field and Heusser 1954	description, survey and photographs	
1953	Heusser 1956	detailed description, survey and photographs	
1953	Field 1979	detailed description, survey, photographs	

Only the more important information sources are shown in this table. The following authors make brief references to the Southeast Lyell Glacier: Woolley 1903, Ostheimer 1928, Munday 1932, and Kramer 1941. Photographs of the glacier are found in Lang 1943 and Meek 1948.

Summaries of the chronology of the Southeast Lyell Glacier are found in Wheeler 1932, Field and Heusser 1954, Heusser 1956, Mercer 1958, Viereck 1968, Denton 1975, Ommanney 1977, Muller 1977 and Field 1979.

1 This does not include the aerial photograph coverage which started in 1947. (See Appendix 1-2A).

TABLE 1-5

SUMMARY OF CHRONOLOGICAL INFORMATION FOR THE SOUTHEAST LYELL GLACIER TRANSECTS [1]

Transect	Approximate Distance From 1984 Glacier Terminus (m)	Age of Oldest Woody Specimen (years)	Species Name of Oldest Plant	Date When It Was Established (years)	Approximate Date of Deglaciation (years)	Approximate Surface Age [2]
1a	20	3	Dryas drummondii	1981	1978	6
1b	20	3	Dryas drummondii	1981	1978	6
2a	70	23	Abies lasiocarpa	1961	1962	22
2b	90	20	Abies lasiocarpa	1964	1960	24
3a	560	34	Salix sp.	1950	1946	38
3b	580	34	Salix sp.	1950	1946	38
4a	1110	28	Picea engelmannii	1956	1941	43
4b	1130	28	Picea engelmannii	1956	1940	44
5a	1240	39	Picea engelmannii	1945	1938	46
5b	1300	45	Picea engelmannii	1939	1935	49
6a	1480	45	Picea engelmannii	1939	1932	52
6b	1510	45	Picea engelmannii	1939	1930	54
7a	1610	49	Picea engelmannii	1935	1920	64
7b	1650	50	Picea engelmannii	1934	1917	67
8a	1700	63	Picea engelmannii	1921	1906	78
8b	1755	63	Picea engelmannii	1921	1902	82
9a	1880	72	Picea engelmannii	1912	1898	86
9b	1890	81	Picea engelmannii	1903	1892	92
9c [3]	1875	101	Picea engelmannii	1883	1875	109
10a	1980	122	Picea engelmannii	1862	1855	129
10b	1980	111	Picea engelmannii	1873	1855	129
11a	2045	139	Picea engelmannii	1845	1841	143
11b (Terminal Moraine)	2045	131	Picea engelmannii	1853	1841	143
12a	2065	432	Picea engelmannii	1552	Unglaciated	432 +
12b (Old Growth Forest)	2090	432	Picea engelmannii	1552	Unglaciated	432 +

1 Where a "ditto mark" is shown, it means that the growth-ring specimens were collected between the "a" and "b" transects, and so it is represented by data from the "a" transect.

2 This is based on growth-ring data, plus aerial photography and published sources (surface age may be older than oldest plant).

3 Although closer to the glacier than Transects 9a & 9b, 9c is more developed because it is closer to the valley side, more protected.

become established at each site.

At the Southeast Lyell Glacier site, approximately 12 years are needed after a surface is exposed before conifer seedlings are established. This factor is probably accurate for the trees that become established on the older moraines. However, after 1930 when the climate became warmer (Gardner 1972), and the ice mass was dwindling, the microclimate adjacent to the glacier probably became less rigorous, so that seedlings would become established in a shorter period of time. This fact is confirmed at some of the sites on younger surfaces. Using air photograph records, and the age of the oldest woody plants on some surfaces, it is impossible for 12 years to have passed before recruitment occurred. Heusser's dates are probably accurate for surfaces deglaciated before 1920, after that, other records such as aerial photographs are more accurate for determining date of deglaciation. Although Heusser did not produce maps with his publications on glacial history (Heusser 1956, Field and Heusser 1954), I contacted him and was able to obtain data from his field notes. The tree ages that were obtained from the 1984 field season correspond closely with those provided by Heusser (pers. comm.).

Heusser (1956) dated the former maximum position of the glacial terminus at 1840 by an ice-tilted tree along the northeast edge of the terminal moraine. Heusser (1956) states that this advance was the greatest expansion of the glacier in several centuries. Presently living trees in the old forest along the north side of the Glacier River, less than 30 m from the terminal moraines, started growing as early as 1552 (Appendix 1-2A). Old rotting trunks lying on the forest floor indicate that the site has been undisturbed for a very long time. The advance of 1840 is probably the furthest downvalley position of the Southeast Lyell Glacier in neoglacial times. During its maximum extent, the glacier encroached upon, but did not entirely override a 45 m high rock promontory near its terminus (Heusser 1956). Recession from the terminal moraine began in 1841. By 1845 some *Picea engelmannii* seedlings were

established on the moraine, as revealed by tree growth-ring data collected in 1984 (Table 1-5, Figure 1-4, Appendix 1-2A).

While retreat of the ice started on the north side of the river in 1841, on the south side it did not start until about 1855, while the earliest retreat from the top of the rock promontory was in 1855 (Heusser 1956). Behind the terminal moraine, Heusser indicates that five poorly-defined moraines were formed about 1855, 1885, 1894, 1902 and 1905 (Figure 1-5). These dates correspond with the data from tree-cores collected during the 1984 field season (Figure 1-4).

During his visit in 1858, Hector (1860) noted that the glacier terminus was only about 90 m upvalley of the terminal moraine. The terminal moraine was quite large, stretching 600 m across the valley bottom, abutting the rock promontory on the south, and the valley wall on the north.

The Southeast Lyell Glacier has shrunk enormously in the past 50 years (Field and Heusser 1954). The total overall recession since 1841 has been approximately 2050 m (14.3 m annually) (Table 1-6). The recession has been in three distinct phases, as described below. The first period was from 1841 to 1926 during which recession was slow, averaging 4.4 to 5.7 m annually for a total of 400 m. In the middle part of this century (1926-1953) recession was very rapid, reaching an annual rate of 51.9 m between 1940 and 1953 for a total recession of 1200 m. Since 1953 the rate of recession has slowed down substantially, so that since 1977 it has averaged only 2.9 m a year along the northeast margin.

In 1902, J. Outram (1905) observed that the Southeast Lyell Glacier was joined by the Mons Glacier near its terminus, compressed between the slopes of Mt. Forbes to the south and the rock promontory to the north. By 1918 the Mons Glacier has receded so that it was at least 300 m from the Southeast Lyell Glacier as recorded on the survey maps by the

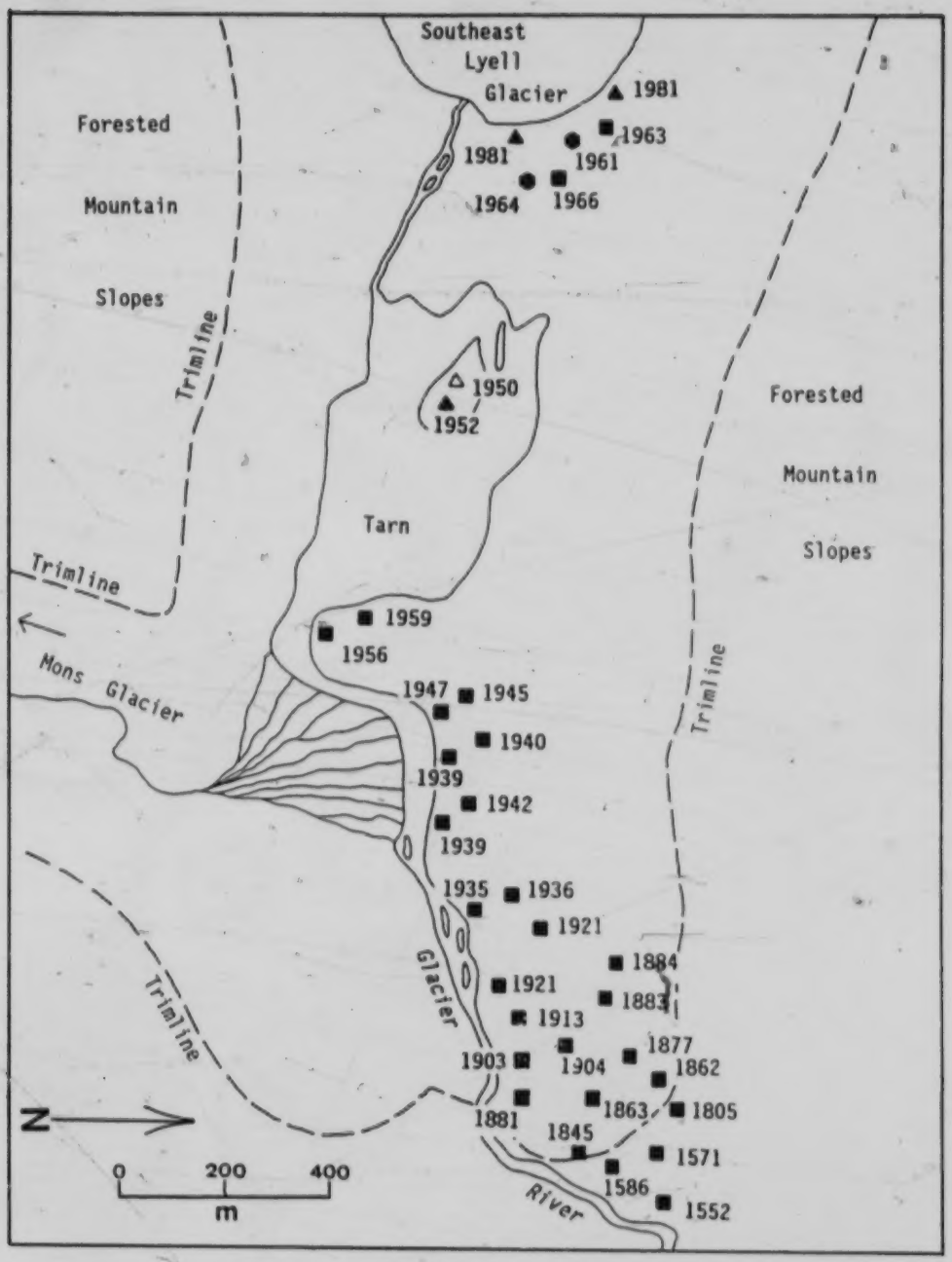

Figure 1-4 Date of Establishment of Oldest Woody Plants Along Southeast Lyell Glacier Chronosequence

LEGEND

▲ *Dryas drummondii*
■ *Picea engelmannii*
⬢ *Abies lasiocarpa*
△ *Salix spp.*

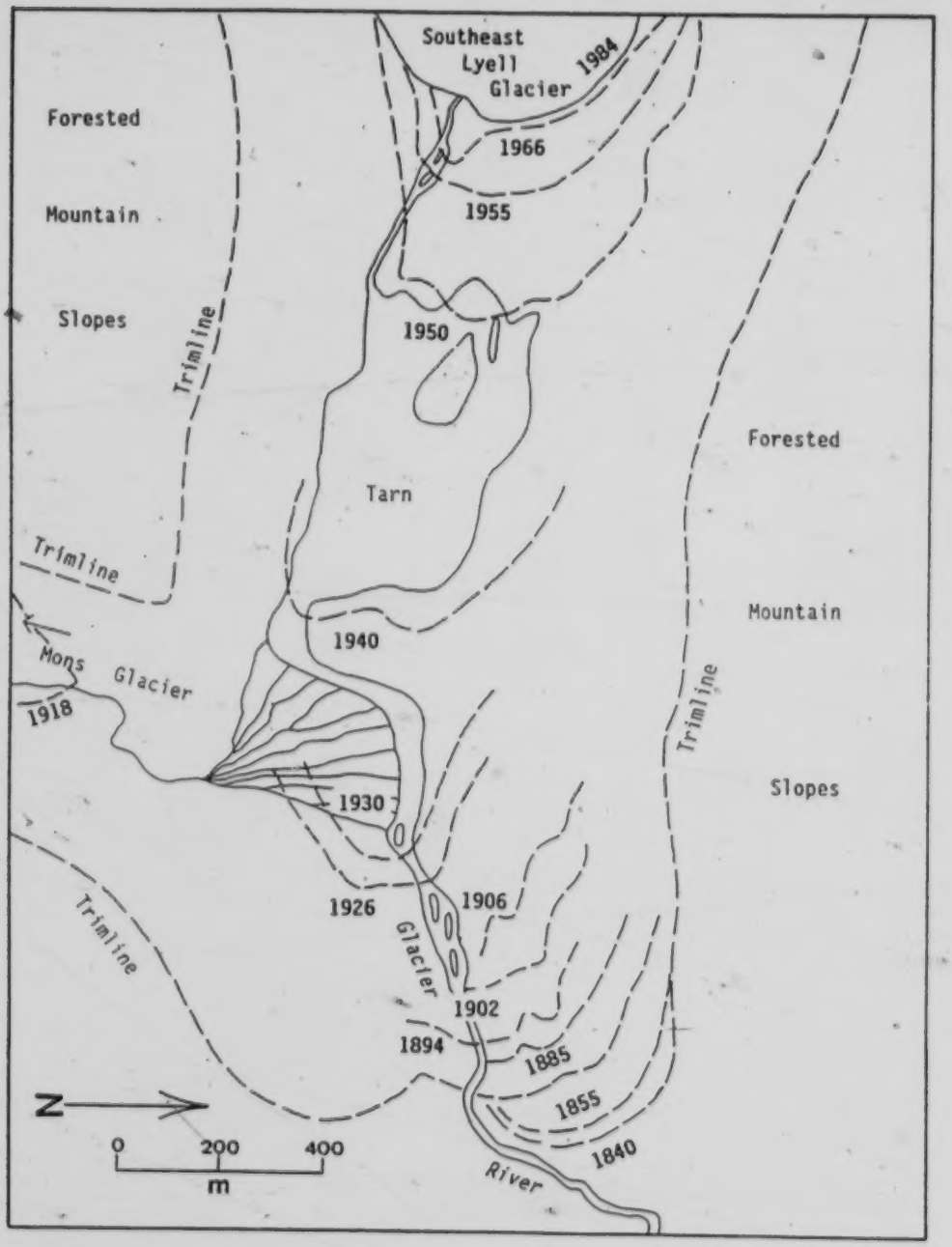

Figure 1-5 Southeast Lyell and Mons Glacier Chronology

Basis for Position Lines:
Dendrochronology: 1840, 1855, 1885, 1894, 1902, 1906
Field Survey: 1926, 1930, 1984
Air Photos: 1950, 1955, 1966, 1977
Ground Photos: 1940

Interprovincial Boundary Commission (1925). By 1953, the Mons glacier has receded far up its valley, so to be scarcely visible from the valley floor. Its recession since 1918 was estimated in 1953 to be 1100 m horizontally and 350 m vertically (Field 1979), which is proportionately greater than that of the Southeast Lyell Glacier (Field and Heusser 1954). Since then its rate of recession has been negligible (Figure 1-5).

In 1926, Thorington (1927b) noted that the Southeast Lyell Glacier had changed little since Hector's visit in 1858 and that its rate of recession was extremely slow; slower than recorded for any other measured glacier in the Canadian Rockies. The rate of recession started to increase in 1926 due to a change in the drainage of the Mons Glacier meltwater stream which caused it to flow against the Southeast Lyell Glacier terminus (Thorington 1927b). In doing so it rapidly eroded it, and carried off large ice chunks weighing tonnes (Thorington 1927b). By 1930, the stream erosion had caused a further retreat of 35 m (Thorington 1931a) for an average of 8.8 m annually (Table 1-6), which was almost two times as great as the 4.7 m annual average since 1841[1].

During much of the 1930's and 1940's the glacier snout rested in a terminal lake. This situation, along with a general climatic warming in the area during those decades (Gardner 1968) resulted in the rapid rate of retreat (Table 1-6, Figure 1-5). In 1944 Thorington (1945a) noted that the tongue ended in a 90 m long lake, with large icebergs calving off the glacial terminus. By 1953 the terminus was 60 m beyond the lake shore and some 4 m above the lake surface at an altitude of 1492 m (Field 1979). Since then, the glacial retreat has almost stopped. This may be due to several factors such as delayed response to the climate cooling in the 1960's (Gardner 1968) plus the fact that the ice terminus now rests on land. It may also be that the glacier is near equilibrium with the warmer climate as mentioned earlier. The rate of retreat is

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[1]According to Ommanney (1977), Thorington erroneously gives the total recession for 1926-1930 as 76 m.

variable along the margin. At the point where the Glacier River emerges, the retreat is somewhat faster (Figure 1-5).

In conjunction with the great amount of horizontal shrinkage, there has been great lateral contraction and subsidence (Thorington 1945b). In 1953, the crests of the north and south lateral moraines were 208 m and 204 m, respectively above the terminus (Field 1979), so at that time, the glacier had downwasted at least 200 m since 1840.

1.3.4.2 Athabasca/Dome Glaciers and Sunwapta River Terrace Chronology

The Athabasca Glacier has been one of the most studied glaciers in the Canadian Rocky Mountains during the past 40 years (see Ommanney 1976). In 1945, detailed surveys of run-off, glacier movement, and glacier variation were begun by the Dominion Water and Power Bureau of the Government of Canada (Denton 1975). Since 1950, government agencies such as the Water Survey of Canada have produced reports on the surveys of the Athabasca Glacier every two years (Water Survey of Canada 1982). This is supplemented by aerial photography coverage of the region started in 1938 (Appendix 1-1B). In spite of all the attention spent on the Athabasca Glacier, there has never been a scientific study on the nearby Dome Glacier (Ommanney 1976), probably for several reasons. It is a smaller, poorly nourished glacier, with an ill-defined snout compared with the Athabasca Glacier (Denton 1975). As well, much of the glacier surface near the terminus is covered with morainal debris.

The Columbia Icefield was not documented until 1896 when it was first visited by Walter D. Wilcox (Harmon and Robinson 1981). In 1903, Hugh Stutfield and J. Norman Collie published a brief description and sketch map of the Dome and Athabasca Glaciers, based on an 1898 climbing expedition. At that time the two glaciers coalesced, forming a solid ice front across the Sunwapta River valley (Figure 1-6). Until 1945 the record of glacial retreat was in photographic form (Table 1-7), at which

TABLE 1-6

RATE OF RECESSION OF THE SOUTHEAST LYELL GLACIER

Interval Period	Total Recession (m)[1]	Annual Average (m)	Distance From Terminal Moraine (m)	Method of Measurement
1841 - 1858	90	5.3	90	direct observation
1858 - 1919	270	4.4	360	ground photos
1919 - 1926	40	5.7	400	direct observation
1926 - 1930[2]	35	8.8	435	direct survey
1930 - 1940	490	49.0	925	ground photos
1940 - 1953	675	51.9	1600	direct survey
1953 - 1977	430	17.9	2030	air photos
1977 - 1984	20	2.9	2050	direct survey
1841 - 1984		14.3	2050	

Sources: Field and Heusser 1954
Muller 1977
Ommanney 1977
Field 1979

1 Estimated to the nearest 5 m.

2 According to Ommanney (1977), published reports by Thorington (1927a, 1927b, 1931a, 1931b) erroneously give the 1926-1930 total recession as 76 m.

TABLE 1-7

INFORMATION SOURCES FOR THE DOME AND ATHABASCA GLACIERS AND SUNWAPTA RIVER TERRACE CHRONOLOGY [1]

Date of Information	Author, Publication Date [2]	Type of Information	General Comments
1898	Stutfield and Collie 1903	brief description and sketch map	Athabsca Glacier descended to valley bottom. Dome and Athabasca coalesced.
1907	Schaffer 1908	photograph of Athabsca Glacier	
1919	Thompson 1920	photograph of Dome and Athabasca Glaciers and outwash	glaciers separated.
1919	Interprovincial Boundary Commission 1925	glaciers mapped (Sheet No. 22 at 1:62,500) and photographed	glaciers separated by about 300 m
1922	Field 1949	photograph of Athabasca Glacier and outwash	
1937	Gibson 1938	photograph of Dome Glacier and outwash	Sunwapta River starting to incise into outwash
1940's	Lang 1943	photograph of Sunwapta River terraces	Terraces "C" and "D" are dry, above floodplain
1940's	Meek 1948	photograph of Athabasca Glacier and outwash	Sunwapta Lake forming
1948	Field 1949	survey, photographs and detailed description	Sunwapta River downcutting, Terraces A, B and C forming
1953	Field and Heusser 1954	survey and photographs	
1953	Heusser 1956	photographs and detailed description	
1971	Cooper 1972	photograph of glaciers and outwash	
1945 - 1980	Water Survey of Canada 1982	detailed survey and photographs of Athabasca Glacier	This is one of the latest government surveys, for a complete listing since 1945 See Ommanney (1976)

Summaries of the chronology of the Dome Glacier are found in Field 1949, Field and Heusser 1954, Heusser 1956, Mercer 1958, Viereck 1968 and Denton 1975. Summaries of the Athabasca Glacier chonology are found in all of the above plus Wheeler 1932, Ommanney 1977, Muller 1977 and Water Survey of Canada 1982.

1 This does not include the aerial photograph coverage which started in 1938 (see Appendix 1-2b).

2 Only those sources which have some relevance to the study site are shown here. Numerous other studies have concentrated solely on the Athabasca Glacier (Ommanney 1976).

time the Canadian Government surveys began (Water Survey of Canada 1982). In 1953, an American Geographical Society survey party visited the area, and using dates based on tree cores, provided the first detailed chronology for these glaciers (Heusser 1956).

In contrast to the factor of 12 years for the Southeast Lyell Glacier site, Heusser uses a 17 year period for trees at the Columbia Icefield to become established on a surface once it became deglaciated. This is probably a function of the colder and more windy climatic conditions at the Columbia Icefield. While in some cases this factor may be correct, on more stable protected surfaces less time is probably needed for recruitment. For example, the new Icefield Parkway was constructed in 1960 (B. Luckman pers. comm.). The 1984 age of many of the trees and shrubs growing on the rocky berm along the highway was 22 to 24 years old, meaning that recruitment occurred very soon after disturbance. As well, shrubs such as *Shepherdia canadensis* and *Salix* spp. are often much older than conifers on the same site (see Tables 1-8, 1-9, Appendices 1-2B, 1-2C). For the following discussion, only the actual tree ages derived from Heusser's study will be used.

According to Heusser (1956) both the Dome and Athabasca Glaciers advanced twice during the past few centuries. The first advance was in the mid 1700's, while the second one occurred a century later. Based on the age of an ice-tilted tree, the Athabasca Glacier reached its first maximum in 1731. Using the age of a tree growing inside the trimline on the northeastern side of the valley, recession started in the terminal area by 1738. After a period of recession, the Athabasca Glacier readvanced sometime in the first half of the nineteenth century, almost to the extent of the earlier one. Recession from this second advance began in 1858 in the terminal area, and has continued ever since (Heusser 1956).

The common source region and the similar location shared by the Athabasca and Dome Glaciers indicates that they both had two periods of

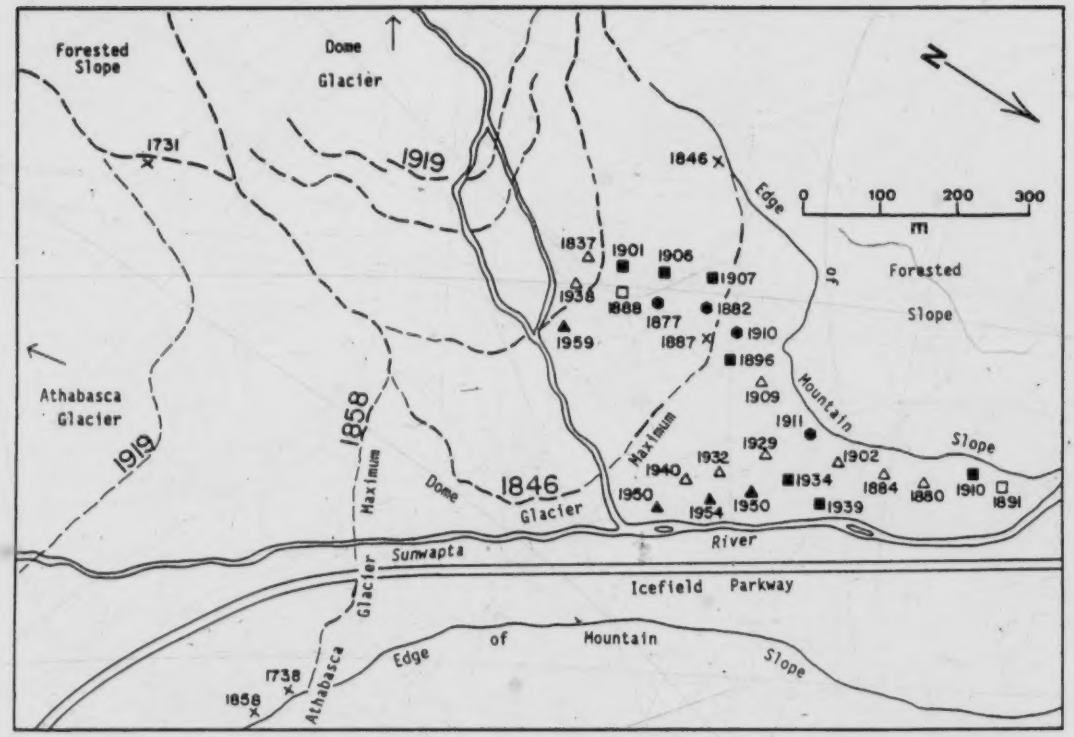

Figure 1-6 Dome Glacier Chronology and Date of Establishment of Oldest Woody Plants

LEGEND

▲ *Dryas drummondii*
■ *Picea engelmannii*
⬢ *Salix glauca* var. *villosa*
□ *Salix vestita*
△ *Shepherdia canadensis*
— — Moraine Positions
— — Inferred Ice Margins

Other Dates from B. Luckmann (pers. comm.) and Jozsa et al. (1983)

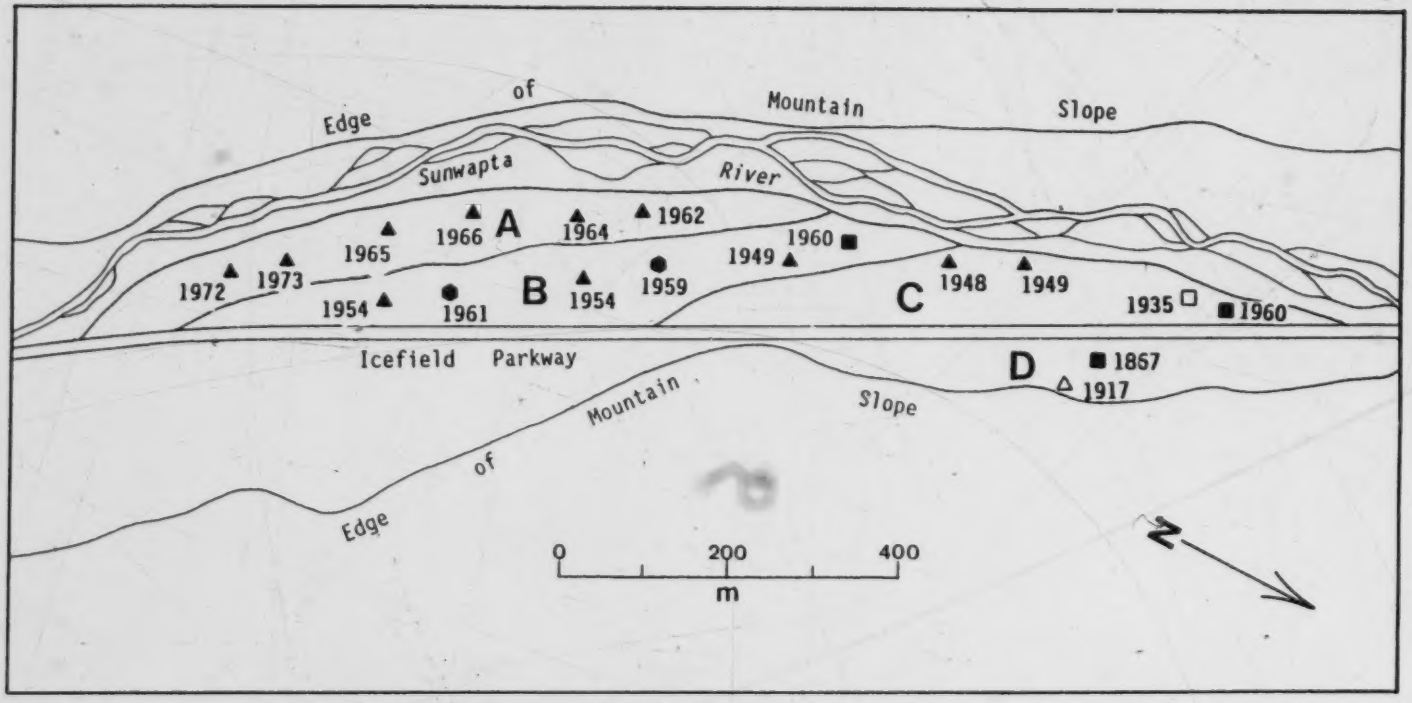

Figure 1-7 Sunwapta River Terrace Chronology and Date of Establishment of Oldest Woody Plants

LEGEND

A,B,C,D - Terrace Surface
▲ *Dryas drummondii*
□ *Arctostaphylos uva-ursi*
△ *Shepherdia canadensis*
□ *Picea engelmannii*
● *Salix glauca* var. *villosa*

advance (Heusser 1956). However, any evidence of an 18th century maximum by the Dome Glacier was obliterated by the second advance, which overrode it. There are no ice-tilted trees to accurately date the time of this second maximum advance. The datable maximum of Dome Glacier is only known from retreat dates.

The botanical evidence for the glacial chronology of the Dome and Athabasca Glaciers is not nearly as substantial as for the Southeast Lyell Glacier site for the following reasons (Heusser 1956): 1) Much of the terminal and recessional moraines for both glaciers has been either reworked or washed away by glacial meltwaters. Interpolation between disconnected piles of morainal debris is used to approximate ice-front positions for particular dates. 2) Shrubs and conifer saplings are only sparsely distributed on the older surfaces. This paucity of information is exacerbated by a lack of written information and early photographs.

Most of the published information gives the date of initial recession from the 19th century maximum as 1870, based on a tree aged by Heusser as having become established in 1887 on the terminal moraine (Heusser 1956, Denton 1975) (Figure 1-6). However, Brian Luckman has done some dendrochronological work in the area in recent years. He found a tree growing in a thin wedge of till against the north valley wall. which began growing in 1846 (B. Luckman pers. comm.). This then is the earliest date of retreat of the Dome Glacier, which corresponds closely with that for both the Athabasca and Southeast Lyell Glaciers. He says that most of the other moraines cannot be dated due to lack of trees. Heusser (1956) estimated the dates of four recessional moraines as approximately 1900, 1908, 1913 and 1918 although he is not able to locate them on a map now (C. Heusser, pers. comm.). The 1919 position is known from the photographs and surveys of the Interprovincial Boundary Commission (1925). At that time, the Dome and Athabasca Glaciers were separated by about 300 m (Figure 1-6).

Recession from 1846 to 1919 was 533 m (7.3 m annually) for the Dome Glacier. During that same time the Athabasca Glacier has receded only 275 m (Field and Heusser 1954). From 1919 to 1953 the situation was reversed, with the Dome receding only 320 m (9.4 m annually), while the Athabasca Glacier receded 822 m (24.2 m annually) (Field and Heusser 1954). The Athabasca Glacier may have responded more slowly to the climatic trend due to its larger size (Field 1949). Since 1953 the rate of recession of both glaciers has slowed down considerably, as was the case for the Southeast Lyell and other glaciers in the vicinity (Gardner 1972, Muller 1977, Water Survey of Canada 1982).

Because both the Dome and Sunwapta study sites are on the glaciofluvial outwash further downstream of the maximum 18th and 19th century glacial advances, the preceding chronology is not directly applicable. Both are located on the Sunwapta Valley outwash, deposited during shrinkage of the Dome and Athabasca since the mid 1800's (Kucera and Henock 1978). Using growth-ring analysis of shrubs and conifer saplings, plus geomorphological and photographic evidence, an accurate chronology is available for those two sites.

In the Dome Glacier outwash site, there is a trend toward older surface ages from east to west. This is because the Dome Glacier outlet stream migrated away from the valley wall, east to its present position. As a result, the local topography slopes very gently to the east. As the stream shifted, higher channels became dry, resulting in "zones of abandonment" (B. Luckman pers. comm.). On the older surfaces, there are areas of more recently disturbed outwash, which represented locations where stream channels were active for a longer period of time, so that the surface age does not run consistently from younger to older (from south to north). However, this is generally the case (see transect sequence in Figure 2-5).

This surface does not appear to have been disturbed by the Sunwapta River for a long time. In this vicinity the river is incised three to

four metres into the surrounding surface. The ages of the oldest woody plants confirm this chronological sequence. The oldest surfaces near the valley wall became stable about 100 years ago. Aerial photography from 1949 show these older surfaces to be totally stable and well vegetated by *Dryas drummondii*. The youngest surfaces near the present stream channel are only 30 years old (Figure 1-6). Interestingly, most of the oldest plants in the area are shrub species (e.g., *Shepherdia canadensis* and *Salix vestita)* rather than conifers (Appendix 1-2B). Table 1-8 and Figure 2-5 gives the approximate ages and locations of all the transects.

The second site is on the Sunwapta River terraces 0.2 km to 1.3 km downvalley from the Dome Glacier outwash. The Sunwapta River location is cut into four terrace surfaces. Table 1-10 gives their age, size and height above the presently active floodplain. Terrace D is the oldest terrace, with one *Picea engelmannii* growing on it found to be 117 years old (Table 1-9). This terrace is close to the northeast valley wall, and has been cut off from active erosion by the old Banff-Jasper road, which was built in that area in 1937 (Gibson 1938) and the Icefield Parkway completed in 1960 (B. Luckman pers. comm.).

The three younger terraces were formed due to the relations between load and river volume, rather than base level changes (Kucera and Henock 1978). In the past 50 years, a proglacial lake named Sunwapta Lake has formed at the Athabasca Glacier terminus. Acting as an effective trap for coarse debris carried by the glacial meltwater (Wankiewicz 1979), it started to form in 1938, and reached its maximum size in 1966 (Kucera and Henock 1978). After 1938, only the Dome Glacier meltwater deposited coarse debris into the Sunwapta River, consequently, the river has excess energy and is now incising into the former outwash surface. This has created a terrace surface 4.0 m high by the Dome Glacier site, although further downstream the river has only cut 2.0 m into the deposits. Terraces A, B, and C have been formed at approximately 18 years, 30 years and 47 years before present (Figure 1-7) (based on

TABLE 1-8

SUMMARY OF CHRONOLOGICAL INFORMATION FOR THE DOME GLACIER TRANSECTS

Transect	Percent Total Dryas drummondii crown cover	Percent Live Dryas drummondii crown cover	Distance from West Valley Side (m)	Species Name of Oldest Plant	Date When Plant Was Established[1]	Minimum Surface Age (based on Plant Age)[2]
Dome-1	4.7	4.4	240	Dryas drummondii	1950	34
Dome-2	54.1	50.8	210	Dryas drummondii	1949	35
Dome-3	30.1	27.6	120	Picea engelmannii	1948	36
Dome-4	17.7	13.9	180	Shepherdia canadensis	1940	44
Dome-5	75.5	49.3	150	Shepherdia canadensis	1932	52
Dome-6	85.4	54.3	85	Shepherdia canadensis	1929	55
Dome-7	79.9	50.6	60	Shepherdia canadensis	1924	60
Dome-8	82.6	54.8	25	Shepherdia canadensis	1902	82
Dome-9	95.5	58.8	15	Salix vestita	1891	93
Dome-10	88.3	41.5	35	Shepherdia canadensis	1880	104

1 This also corresponds to the latest time when the surface became stabilized at that location.

2 This is a conservative estimate of surface age, based on the age of the oldest existing wood plant.

TABLE 1-9

SUMMARY OF CHRONOLOGICAL INFORMATION FOR THE SUNWAPTA RIVER TRANSECTS

Transect	Percent Total Dryas drummondii crown cover	Percent Live Dryas drummondii crown cover	Species Name of Oldest Plant	Date When It Was Established [1]	Minimum Surface Age (Based on plant age) [2]
A-1	3.5	3.5	Dryas drummondii	1972	12
A-2	2.2	2.2	Dryas drummondii	1965	19
A-3	3.3	3.2	Dryas drummondii	1962	22
B-1	15.3	13.5	Dryas drummondii	1957	27
B-2	53.8	50.4	Dryas drummondii	1954	30
B-3	42.8	35.9	Dryas drummondii	1954	30
B-4	71.5	61.7	Dryas drummondii	1949	35
C-1	73.9	58.7	Dryas drummondii	1948	36
C-2	75.9	63.6	Arctostaphylos uva-ursi	1935	49
D-1	78.6	66.4	Picea engelmannii	1867	117

1 This also corresponds to the latest time when the surface became stabilized at that location.

2 This is a conservative estimate of surface age, based on the age of the oldest existing woody plant.

TABLE 1-10

SUMMARY OF RIVER TERRACE INFORMATION FOR THE SUNWAPTA RIVER SITE

Terrace	Age (Dates)	Height Above Presently Active Floodplain (m)	Number of Transects Sampled	Width and Length [1]
A	15-20 years 1962-1956	0.5 - 1.0	3	50-75 m wide 0.9 km long
B	27-35 years 1942-1954	1.5 - 1.7	4	100-150 m wide 0.9 km long
C	45-50 years 1935-1940	2.0 - 2.3	2	100 m wide 0.8 km long
D	115 years 1867	2.5	1	70 m wide 0.7 km long

1 The measurements for terraces A, B and C apply only to those portions southeast of the Icefield Parkway.

The floodplain is 70 m to 200 m wide in this area.

growth-ring counts and aerial photography evidence) as the river has cut into the deposits while shifting toward the southwest valley wall. Aerial photographs indicate that terrace surfaces were not abandoned all at once, rather, there were "zones of abandonment" as is the case at the Dome Glacier site. For example, Terrace A was totally covered by active channels in 1949, partly stable in 1966 and not fully abandoned until 1972. However, these terrace surfaces are reasonably well defined and are separated by terrace risers 0.5 to 1.0 m in height (Table 1-10).

1.3.5 Geomorphology

1.3.5.1 Southeast Lyell Glacier Site

The Upper Glacier River, where the Southeast Lyell Glacier study site is found, is contained within a narrow U-shaped canyon valley. The slope of the valley walls is bedrock controlled, with large amounts of bedrock exposed. The actual Southeast Lyell site is contained within the trimline of the maximum Neoglacial advance, thus almost all the genetic material is either glacial in origin or strongly modified by glacial action.[2]

Within the trimline, areas of bedrock exposure are mostly limited to areas south of the Glacier River, except for a portion near the present day terminus (Figure 1-8). The bedrock is exposed as NW-SE trending ridges, dipping to the southwest, often with unconsolidated material lodged between the ridge crests. The most prominent bedrock outcrop is the large 45 m high rock bluff on the south side of the Glacier River near the terminal (end) moraine. Thorington (1927a) called it a "Gibraltar in miniature" while Heusser (1956) said it looks like a

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[2]According to Walker et al. (1982a), glacial deposits are those directly associated with ice contact processes. They include morainal material (till) and ice contact stratified drift (e.g., eskers). Proglacial deposits (e.g., glaciofluvial and glaciolacustrine) are formed beyond the glacier terminus.

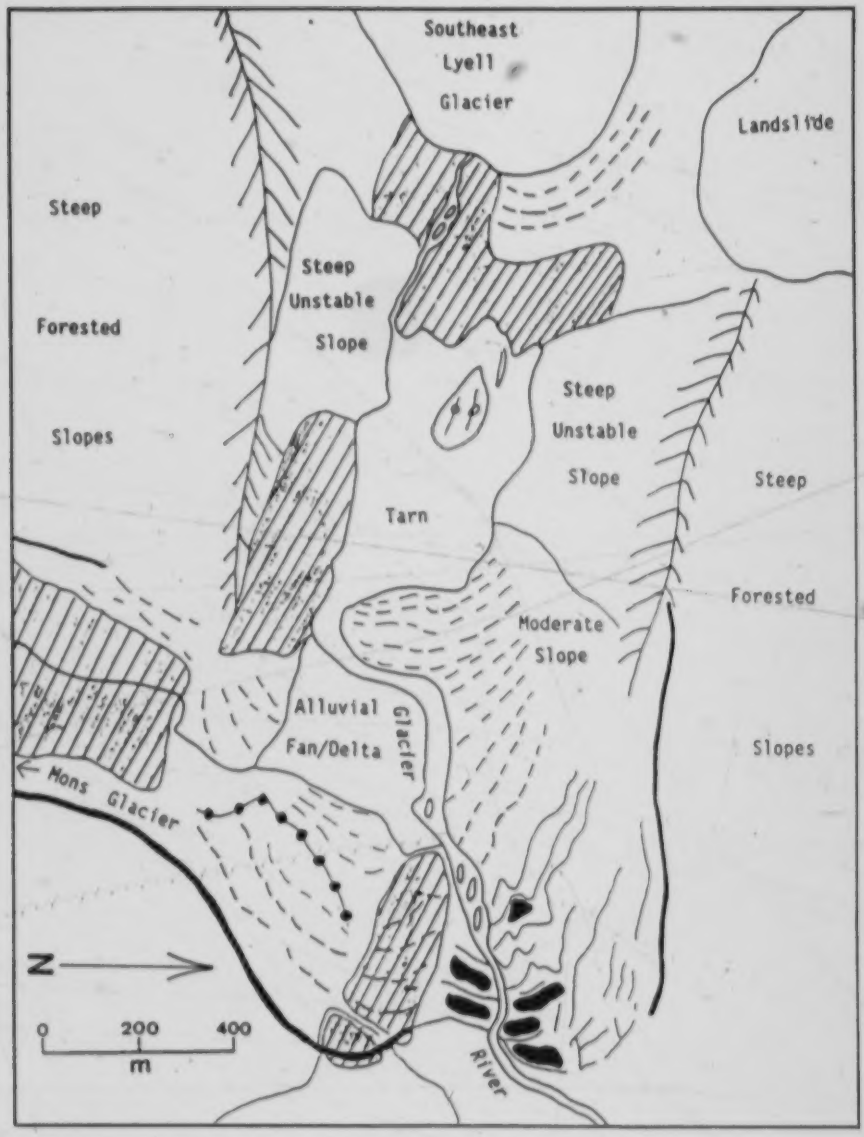

Figure 1-8 Geomorphology: Southeast Lyell Glacier Site

LEGEND

- Lateral Moraine
- Large Moraine Ridge
- Small or DeGeer (Annual) Moraine
- Hummocky Recessional Moraine
- Esker
- Fluting
- Bedrock
- Trimline

massive *roches moutonnees*, with its stoss side inclined toward the glaciers and the lee side oriented along the axis of the valley. To the south, the valley that contains the Mons Glacier is a very steep, V-shaped gorge, mostly composed of exposed bedrock.

Most of the unconsolidated genetic material forming the study area surface is morainal in origin, interspersed with glaciofluvial deposits. Because of the nature of the source material (medium to fine grained, calcareous rock strata), the deposits are extremely calcareous and neutral to mildly alkaline (Walker et al. 1982a). The till is a diamicton, meaning that it contains an unsorted matrix of widely varying particle sizes, from clay to boulder size. It is exceedingly stony, with 40 - 70% coarse fragments (gravel, cobble, stone) and is analogous to the "Till C" of Walker et al. (1982a, p. 37) which is characterized by medium textured silty loam to loam.

The glaciofluvial deposits found at the study site are calcareous and coarse textured, which is analogous to "Glaciofluvial Material B" of Walker et al. (1982a, p. 45). The fine earth fraction is loamy sand to sand in texture because silts and clays are removed in the glaciofluvial environment.

The terminal and recessional moraines are well developed at this site, especially north of the river. The terminal moraine, stretching 600 m across the valley floor, is breached by the Glacier River and several abandoned meltwater channels (Figure 1-8). It is 2-3 m high on the downvalley side and up to 6 m high on the upvalley side. Near the terminal moraine is a series of large recessional moraines, ridged to hummocky in form, and 3 to 7 m high. They were formed in the 1800's when the glacier ice front was slowly receding. During this time there was probably substantial meltwater action as the heavily debris-laden ice wasted. Consequently, the recessional moraines are not well defined. Heusser (1956) wrote that the "moraines are chaotic among the abandoned stream channels."

Some of the moraines are ridged while others are broad and hummocky, from 20 to 50 m wide. They are quite stony, with large boulders lodged in the till. The dated moraine surfaces are very heterogeneous in terms of texture and stoniness. In this area near the terminal moraine the valley slopes gently 1°-2° to the east. Located between the moraines are SE-trending abandoned meltwater channels. They are 2-4 m wide where they cross moraines, and expand out into channelled flats, up to 50 m wide between the moraines. They are finer textured than the moraines, with fine to coarse gravels most common. On some of the larger hummocky moraines are closed depressions, often containing silty deposits.

Further upvalley, the recessional moraines become progressively smaller, more ridged (less hummocky) and more widely spaced. This is because the glacier was receding faster on these surfaces. The moraines are medium sized (2-3 m high, 3-8 m wide) and gradually become reduced to small moraines near the tarn. Although the genesis of these smaller moraines is uncertain, they may be De Geer (annual) moraines (Sudgen and John 1976, p. 247) which are formed in winter by the seasonal glacier readvance. In form they are sinuous and parallel, 0.5 - 1.5 m in height, 2 to 5 m wide and spaced 28 - 30 m apart. Between the De Geer moraines are areas of gently rolling ground moraine which blankets the underlying bedrock.

Although there are some abandoned meltwater channels here, they are not as well developed as further down valley. In this location the valley slope is slightly steeper (3°-8°, south and southwest aspect) with one area of moderately steep slope (10°-15°, south aspect) (Figure 1-8). Closer to the present day glacier, the recessional moraines increase in size again, probably because the rate of glacial recession has slowed down. Here the moraines are 0.5 - 2 m tall, irregularly ridged to hummocky and are smeared on the underlying bedrock. South of the river, the moraines are more uniform in size on all the surfaces. They are between 2 and 4 m tall, and about 5 m wide.

In work done on the plant-free recessional moraines of the Athabasca Glacier, Welch (1967) found that frost heaving, rainwash and settling are the main processes of slope alteration. The equilibrium form is a slope of 25°-30° with narrow summits of a convex form. This form is also common at the Southeast Lyell site, although the hummocky moraines are rounded at the top, perhaps due to the effect of vegetation development. The moraine slopes average 25°, although slopes of 40° are common at sites where currently-active meltwater streams impinge on the slope. On plant-free moraine slopes of all ages, processes such as shallow surface colluviation ("mini-slides") and surface sheet erosion are actively altering the slope profile. These moraines do not appear to be ice-cored.

Broad lateral moraines are prominent on both north and south valley walls (Figure 1-8, Plate 1-2). Their ridge crests are 200 m above the valley floor. Because their sides were oversteepened when the glacier filled the valley, they are now unstable, with slope failure, gullying and landslide action exposing areas of bedrock underneath. Seepage zones occur near the base of the lateral moraines and contribute to their instability.

A large tarn (700 m x 350 m) occupies a basin (altitude 1490 m) which was deglaciated in the 1940's (Field 1979). To the east was a second shallow lake, formed in the 1930's (Thorington 1945b). Since then, the Mons Glacier outlet stream has built a large alluvial fan/delta complex which almost fills the lake.

At this site there are a variety of other interesting, glacial and periglacial features:

1. Flutings - on the island in the tarn, at least three flutings run parallel to the direction of ice movement. These features, formed subglacially, are 0.6 to 1.0 m wide, and 13 to 30 m apart with crests 0.3 m above the surrounding ground moraine. They are similar to flutings found in front of the Saskatchewan Glacier in Banff

National Park (McPherson and Gardner 1969) and are probably a feature of glacial deposition (Sugden and John 1976).

2. Esker - South of the Glacier River is a large esker composed solely of sorted boulders 0.5 to 0.8 m in diameter. It is 3 m tall, 5 m across and 150 m long, probably formed by a subglacial stream in the Mons Glacier.

3. Sorted Stripes - These features are located on the exposed surfaces east of the tarn. They are 13 to 20 m in length and trend up and down valley. The stripes are plant-free, composed of fine to medium sized gravels and are surrounded by coarser deposits. The presence of needle-ice in the vicinity indicates that they may be periglacial in origin.

Excluding the presently active stream channels and alluvial fans, most of the study area is moderately well to well drained. The microtopography is quite varied, especially on the older hummocky moraines. In areas of bouldery till, it can range over 1 m in a short space. Closer to the glacier on the ground moraine it is less rough, averaging 0.1 to 0.2 m.

1.3.5.2 Columbia Icefield Site

Like the Southeast Lyell Glacier site, the research locations at the Columbia Icefield are situated wholly within a recently altered glacial environment. In the former case, morainal material is dominant, while here, glaciofluvial outwash is the most common landform. Even within the trimline of the late-Neoglacial maximum of the Dome Glacier, most of the surface has been reworked by meltwater, and outwash deposits are predominant. The moraines are discontinuous and usually in the form of low ridges, 2-3 m high, 4-6 m across. Only a few areas of hummocky ground moraine occur within the Dome Glacier Trimline (Figure 1-9).

Further south and southeast, large areas of recessional and ground moraine deposits are found in association with the Athabasca Glacier.

Reports prepared by Environment Canada, Glaciology Division give a comprehensive overview of the glacier and landform features in the Columbia Icefield area, including maps at a scale of 1:12,500 (Kucera and Henock (1978), Baranowski and Henock (1978). Since both the Icefield research locations are on the proglacial outwash, the following discussion will consider only that landform type. For a more comprehensive discussion of all the glacial landforms in the area refer to the sources mentioned above.

As with the Southeast Lyell Glacier site, the outwash here is defined as "Glaciofluvial Material B" by Walker et al. (1982a, p. 45). It is calcareous and coarse textured, and is derived from the reworking of the calcareous glacial till. As this landform is created by running water, only the coarser sediments are deposited. Consequently, the fine earth fraction has 75% sand content (Walker et al. 1982a).

The glaciofluvial outwash plain of the Sunwapta River Valley is a broad alluvial plain that extends four km northwestward from the Dome and Athabasca Glaciers, between the slopes of Mount Wilcox on the east and the base of Mount Kitchener on the west. This plain tapers northward from 0.8 km wide at the south end to 0.09 km at the north end where the Sunwapta River Canyon begins. The outwash slopes to the northwest at a rate of 30 m/km for the first kilometre. It levels out with a gentler slope of 10 m/km for the next three kilometers (Kucera and Henock 1978). It was formed since the mid 1800's during shrinkage of the Dome and Athabasca Glaciers when large volumes of water from melting glaciers mantled the underlying landscape with these coarse deposits (Walker et al. 1982a).

Although some outwash surfaces in the North Saskatchewan River valley are still aggrading (Smith 1972), the deposits at the Icefield

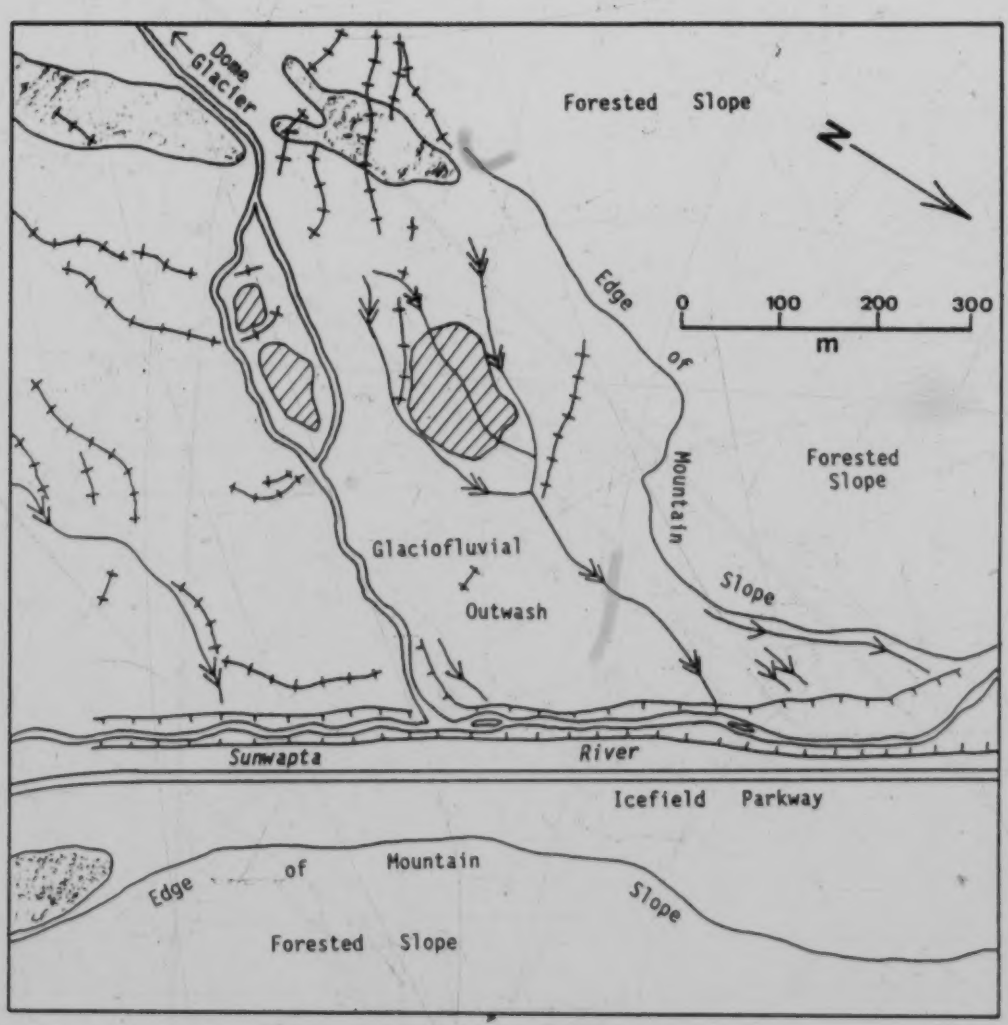

Figure 1-9 Geomorphology: Dome Glacier Site

LEGEND

Stream Channels
- Abandoned
- Intermittent
- Permanent

- River Terrace Riser
- Moraine Ridge
- Non-Ridged Moraine
- Bedrock

are now being incised by the Sunwapta River. As noted earlier in Section 1.3.4.2, Sunwapta Lake acts as a sediment trap. It is 6.5 m deep, 800 m long and fed by three meltwater streams (Kucera 1972). During the summer, no sand leaves the lake, and only 33 ppm of silt and clay is carried out (Baranowski and Henoch 1978), thus over time the lake will fill in. With its smaller sediment load, the Sunwapta River has greater erosional power, and is now cutting into the pre-existing outwash plain.

The Sunwapta River flows across this outwash plain in braided channels. This braided river type is characterized by steep gradients and large loads (Baranowski and Henock 1978). It is composed of many converging and diverging channels with many islands and bars formed from the alluvial deposits. During the winter months, stream flow is confined to a few main channels, while during the summer, meltwater from snow and ice swells the river so that the active floodplain is one quarter to one half the valley bottom width.

The stable glaciofluvial surface above the present floodplain is criss-crossed with numerous abandoned river channels. They are 3-5 m wide and from 0.3 to 0.7 m deep although the largest ones are up to 1 m deep and 15 m across. These channels provide local microrelief in an otherwise level surface. The number of old channels is variable. Some places are mostly smooth gravel surfaces, while others are covered with numerous shallow braided channels.

Although from a distance the outwash appears to be a uniform coarse gravel surface, on closer inspection one can see that it is a complex assemblage of different-sized materials. While medium to coarse gravels are most common, they are intermixed with large areas of cobbles, as well as some sites with finer gravels.[3] Fine textured materials (< 2 mm) comprise less than five percent of the area.

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[3]The size classes for coarse material (based on Walmsley 1980) are as follows: Fines 2 mm, Gravels 2-75 mm, Cobbles 75-250 mm, Stones >250 mm.

The pattern of varying sized deposits is due to the nature of this proglacial environment. Constantly shifting channels, accompanied by variations in water speed and volume, reworked and redistributed the deposits. On the old channel bottom, coarse gravels and cobbles predominate, interspersed with sand deposited in quiet pools and backwaters. The old bars and islands between the channels are characterized by medium sized gravel "pavement" surfaces, in which the fine material has been removed by the water action or by subsequent wind deflation. These surfaces exhibit low microrelief, usually less than 0.1 m.

Presently, most of these surfaces are stable although a few intermittent channels still run along some of the lower surfaces. Over time, the surface microrelief becomes more subdued, due to surface settling and aeolian action, which deposits sand between the larger sized materials. Needle-ice is common in finer textures sand deposits, which offsets the smoothing effect of the processes noted above. This area is well to rapidly drained, causing subxeric conditions. Local microtopography creates some submesic moisture conditions along some of the old channels.

The Dome Glacier outwash site is bounded on the northeast and east by the Sunwapta and Dome Glacier outlet streams, respectively. The slope gradient is in two directions. The main slope (1°-3°) is northeast toward the Sunwapta River, parallel to the abandoned meltwater channels (Figure 1-9). Superimposed on this is a slight slope to the east, formed as the Dome Glacier meltwater stream downcut into the surface as it migrated away from the valley wall (see glacial chronology section).

The Sunwapta River has, since the 1940's, incised 2.5 to 4 m into the Dome Glacier outwash. The Dome Glacier meltwater stream has adjusted to this new base level (the confluence point with the Sunwapta River) by downcutting in its lower reaches.

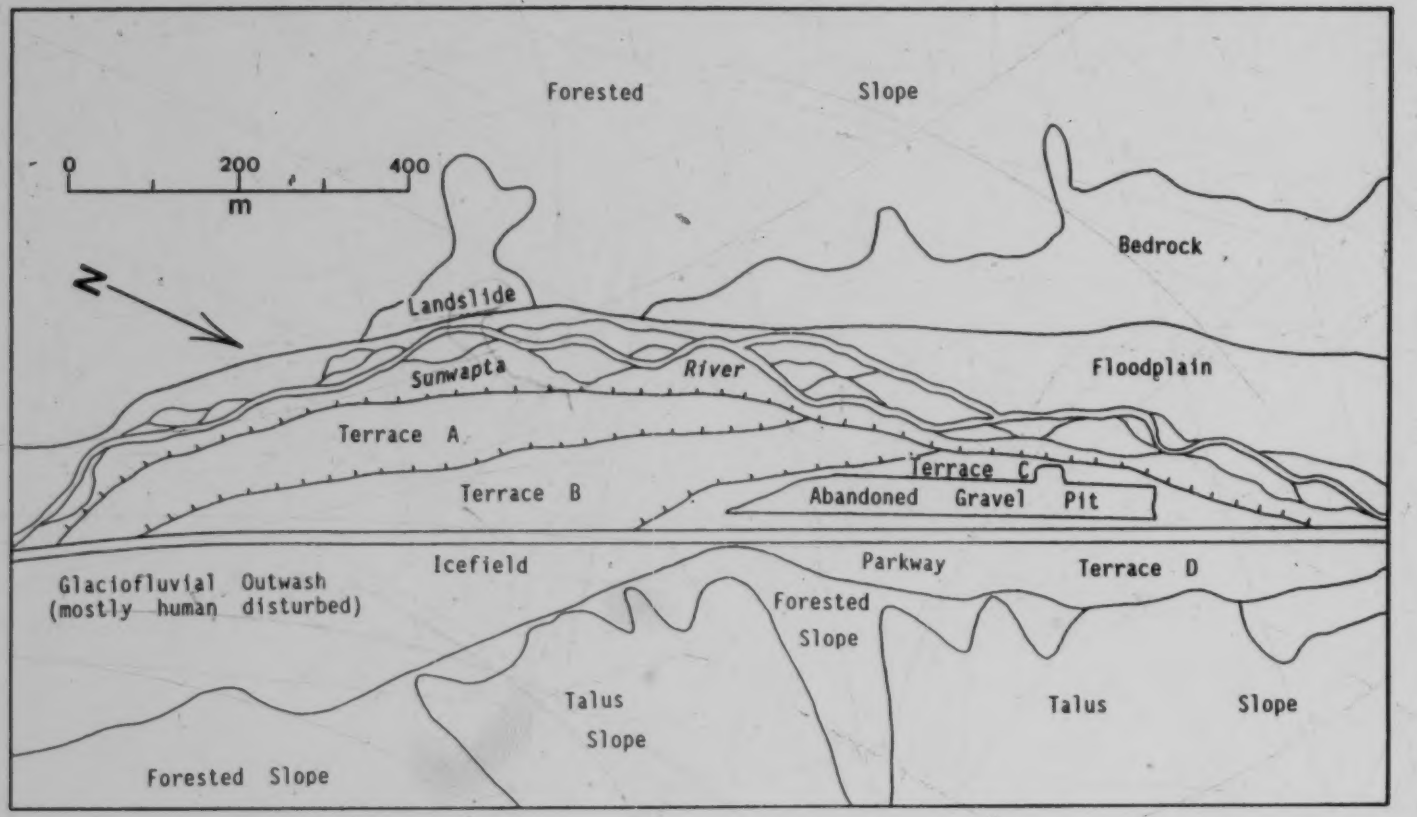

Figure 1-10 Geomorphology: Sunwapta River Site

In contrast to the Dome Glacier outwash site (which could be considered as one channelled terrace surface) the Sunwapta River site is formed of four distinct terrace "treads" (Figure 1-10). These surfaces formed as the Sunwapta River migrated toward the southeast while incising into the outwash surface. The terrace treads are 50 to 150 m wide and 700 to 900 m long (Table 1-10). The slope of the terrace treads is less than 1° and is oriented downvalley (NNW) rather than towards the river. The terrace risers are steep (30° to 70°) and are from .5 to 1.2 m high. The height of a particular riser varies along its length as the difference in height between two adjacent terrace treads can vary.

There are large talus slopes along the northeast valley wall (Figure 1-10). Large stones and boulders litter the outwash surface up to 200 m from the base of the talus cones.

Unlike the Dome Glacier outwash site, the terraces along the Sunwapta River have been disturbed by human activity. The Icefield Parkway, constructed in 1960, runs through the study site. On both sides of the highway right-of-way, there is 5 m of stony berm. As shown in Figure 1-10, during the construction of this highway, a gravel pit (60 m wide, 500 m long, 2.5 m deep) was excavated next to the road on Terrace C. Not shown in this figure is the old Banff-Jasper road which, along with a telegraph line and ditch, ran across Terrace D, parallel to, and just 7 m from the new highway. In conjunction with these road rights-of-way are miscellaneous bladed trails and small borrow pits (indeed, most of the surface across the highway from Terrace B is disturbed. It is easy to tell where the outwash has been altered, as the sinuous braided channel pattern is interrupted.

1.3.6 Vegetation Development

The Southeast Lyell and Columbia Icefield study sites have the same major vascular species (*Dryas drummondii*, *Shepherdia canadensis*, *Salix*

glauca var. *villosa*, *Picea engelmannii* and *Abies lasiocarpa*) although they differ markedly in their overall development. The former site is 400 metres lower than the latter, which is reflected by a warmer and drier climate (see Section 1.3.3); this seems to have a major influence on the vegetation. This section gives a general vegetation description; more detailed discussion is presented in the papers which follow. Appendix 3-6 is a list of all vascular and non-vascular species (along with authority names) occurring at both study areas.

1.3.6.1 Southeast Lyell Glacier Site

The development of vegetation is obvious along the time gradient. Within five years after deglaciation, *Dryas drummondii* becomes established and within 20 years forms an almost continuous carpet (Plate 1-5). The extensive *Dryas* cover here is greater than on any other glacial foreland in the region (Heusser 1956). Tree species such as *Picea engelmannii*[4] and *Abies lasiocarpa* are also established soon after deglaciation. The only herb of any significance on these young surfaces is *Castilleja miniata*, which is a root parasite.

By 40 years, shrubs such as *Shepherdia canadensis* and *Salix glauca* var. *villosa* appear along with lesser amounts of *S. drummondiana* and *S. commutata*. These shrubs, along with the larger *Picea* and *Abies* saplings growing amidst the *Dryas* carpet, give these areas a "park-like" appearance (Plate 1-6). Walker et al. (1982b, p. 511) give a community description of this site and Corns and Achuff (1982, p. 135) provide data on similar plant communities in the region.

Shrub and tree cover, as well as species richness, gradually increases along the time gradient (Plate 1-7). A break in the

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[4] Some of the *Picea* may be hybrids of *P. engelmannii* and *P. glauca*, as shown by crown form. Since this is a lower subalpine site, and *Picea glauca* occurs downvalley (Heusser 1956), this is quite possible.

Plate 1-5 Seral Stage 1: Incipient *Dryas drummondii* Community on 6 Year-Old Recessional Moraine, Southeast Lyell Site. July 1984

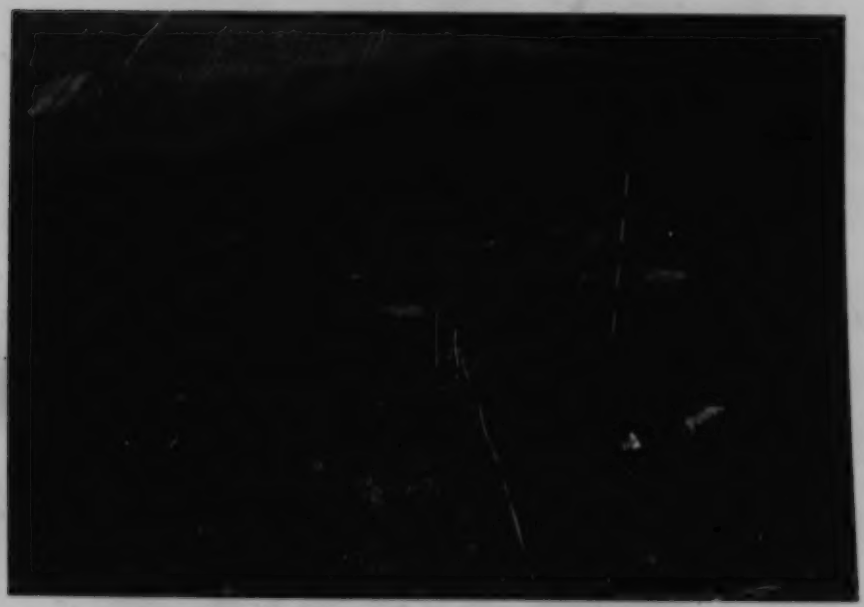

Plate 1-6 Seral Stage 2: *Dryas drummondii* Community on 45 Year-Old Surface, Southeast Lyell Site. July 1984

Plate 1-7 Seral Stage 3: *Picea engelmannii/Dryas drummondii* Community on 65 Year-Old Surface, Southeast Lyell Site. July 1984

Plate 1-8 Early Seral Stage 4: *Picea engelmannii/Dryas drummondii* Community on 100 Year-Old Surface, Southeast Lyell Site. July 1984

developmental sequence appears around year 90 in conjunction with tree canopy closure. At this point, *Dryas* cover starts to decline. This is noted first by dead areas in the continuous carpet, which are often colonized by acrocarpous mosses such as *Bryum caespiticium*, *Ceratodon purpureus*, *Ditrichum flexicaule*, *Tortella tortuosa*, *Tortula norvegica* and *T. ruralis*. These species are also present in the younger *Dryas* communities, but are much less conspicuous.

The community on the 100 year-old surface is a mosaic of open *Dryas* interspersed with more treed areas (Plate 1-8). The terminal moraine (130 year-old) community has mostly a closed forest canopy and a dense shrub stratum: *Dryas* has almost disappeared from the community (Plate 1-9). Although the earlier acrocarpous mosses are still present, total moss cover is increased by the addition of such pleurocarpous species as *Brachythecium groenlandicum* and *Drepanocladus uncinatus*. Lichens (mostly *Cladonia* spp.) appear on more exposed moraine crests.

The adjacent old-growth forest represents a potential end state in this sequence. It has a mixed overstorey of *Picea* and *Abies* with subdominant *Populus balsamifera* (the latter species occurs only sporadically within the trimline) (Plate 1-10). The shrub stratum is still composed mostly of *Shepherdia canadensis* and *Salix glauca* var *villosa*. A well developed bryoid carpet dominated by *Hylocomium splendens*, *Dicranum scoparium* and *Barbiliphozia lycopodioides* is present. Herb species richness is much greater than on the moraines and includes a variety of orchids and other species characteristic of this environment. This community type seems to be self-perpetuating as indicated by the age of some of the trees and the strong *Abies* regeneration.

Vegetation development on a particular surface is by no means homogeneous. The intermediate-aged surfaces, in particular, are characterized by large moraines interspersed with broad abandoned meltwater channels (see Section 1.3.5). Tree cover is most pronounced on

Plate 1-9 Seral Stage 4: *Picea engelmannii/Shepherdia canadensis* Community on 143 Year-Old Terminal Moraine, Southeast Lyell Site. July 1984

Plate 1-10 Old-Growth Forest: *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens* Community, (> 432 Years Old), Southeast Lyell Site. July 1984

the lower moraine slopes, whereas the old channel areas are covered with an almost continuous cover of *Dryas drummondii* along with a few shrubs. Vegetation is more homogeneous, however, on the younger and older surfaces. This is due to fewer meltwater channels on the former surface and infilling by trees on the latter.

There are numerous seepages in the area which support an abundance of *Salix* species, particularly *S. drummondiana*, *S. brachycarpa*, *S. commutata* and *S. glauca* var *villosa*. There is also high moss cover dominated by *Bryum pseudotriquetrum*, *Catoscopium nigritum* and *Drepanocladus revolvens*.

1.3.6.2 Columbia Icefield Site

At the Dome Glacier and Sunwapta River sites, the vegetation on the stabilized glaciofluvial surfaces consists almost entirely of *Dryas drummondii* (average 96% of all plant cover). As at the Southeast Lyell site, it attains almost continuous cover within 20-40 years after surface stabilization. On some older morainal surfaces nearer the Athabasca and Dome Glaciers, the other dryad species, *D. integrifolia* and *D. octopetala* ssp. *hookeriana* x *integrifolia* are also present.

On older stabilized terraces, isolated stunted individuals of the following woody species are present: *Abies lasiocarpa*, *Picea engelmannii*, *Shepherdia canadensis*, *Salix glauca* var. *villosa* and *S. vestita* Pursh, with smaller amounts of *Arctostaphylos rubra* (Rehder & Wils.) Fern. and *A. uva-ursi* (L.) Spreng. Herbaceous plants are rare.

Moss cover is around 2-3 % and includes mostly acrocarpous forms: *Bryum caespiticium*, *Ceratodon purpureus*, *Ditrichum flexicaule*, *Tortella fragilis* and *T. inclinata*. The lichens *Candelariella terrigena* and *C. xanthostigma* and the fungus *Marasmius epidryas* are commonly epiphytic on older *Dryas* clones.

Unlike those of the Southeast Lyell study site, the *Dryas*-dominated communities seem to represent the maximum development in this cold, windy environment. Around 40 years after establishment, the *Dryas* clones start to decay and are broken up and removed by physical action (frost and wind) leaving a bare surface which is eventually re-colonized by *Dryas*. This cyclical succession consisting only of *Dryas* has similarities to a three-phase cyclical succession involving *D. octopetala* on raised beaches in Iceland (Anderson 1967) and is probably related to the harshness of the environment.

On some sheltered locations on nearby moraines, *Picea* and *Abies* are successfully established. Unless there are future changes to the local environment (e.g., climatic warming), the open glaciofluvial terraces will almost certainly continue to support only simple *Dryas*-dominated communities.

1.3.7 Soil Development

A sequence of soils developed on uniform parent materials and landforms and under constant climatic and biotic conditions, in which differences in properties are a function of time is called a "chronosequence" (Stevens and Walker 1970). At both study sites, chronosequences are present because four of the five soil-forming factors (climate, biota, topography, parent material) are kept relatively constant (the exception being time). As noted at Glacier Bay, Alaska (Ugolini 1966), when the vegetation progresses from *Dryas drummondii* to a closed forest canopy and a moss layer becomes established, the biological influence on soil-forming processes is no longer constant. This is true for the Southeast Lyell site in a strict sense, but only on the oldest surfaces.

Chronosequence studies have been most useful in deglaciated areas (Stevens and Walker 1970). Studies from Northwestern North America on

chronosequences (usually several hundred years in length) are particularly numerous and include the following from southwestern Alaska: Chandler (1942), Crocker and Major (1955), Crocker and Dickson (1957), Ugolini (1966); from central Alaska: Viereck (1970); from the Yukon: Jacobson and Birks (1980); and from the Canadian Rockies: Tisdale et al. (1966), Fitter and Parsons (1987), Sondheim and Standish (1983), Howell (1978).

These studies all document the same general trends in soil properties over time. Even with differences in species, the soil--vegetation relationships are similar (e.g., Glacier Bay vs. the Kutlan Glacier (Jacobson and Birks 1980)). However, the development in continental areas (including the study area) is slower, usually by 50 to 100 years (Jacobson and Birks 1980). This is probably due to the colder climate (see Section 1.3.3) and its effect on vegetation development (Tisdale et al. 1966). Deglaciated areas in a more maritime climate have accelerated soil development due to a rapid vegetation growth, and high leaching potential (Ugolini 1966). Indeed, some researchers consider soil-vegetation correlation more important than soil-time relationships in explaining soil development (Crocker and Major 1955). It is a two way interaction in which changes in soil properties are more a function of vegetation development than a function of time itself (Crocker and Major 1955, Jacobson and Birks 1980). It is apparent, when comparing the Southeast Lyell and the Columbia Icefield chronosequences, that the vegetation-climate interactions are most significant.

Vegetation pattern as well as species composition is important. For example, at Glacier Bay, the rate of development for the soil nitrogen profile and other properties such as pH, depend on the pattern of plant distribution (Crocker and Major 1955). The role played by *Dryas drummondii* in soil development at both these sites is fundamental: it stabilizes erosional processes, contributes to LFH and Ah horizon development and increases nutrient and cation exchange capacity in the soil (Wilson 1978).

At the study sites, the most important soil-forming influences are the short time period for soil genesis, high carbonate concentrations, climate (especially microclimate) and rate and direction of vegetation development (especially of nitrogen-fixing species). Despite present surface stability, pedogenic processes have had little effect on the highly calcareous material, therefore there are only Regosols (Walker et al. 1982b, p.510).

The short time since surface stabilization seems to be the primary factor influencing soil development. In soil genesis, there are two general stages: 1) creation of the upper organic horizons due to vegetation establishment, and 2) later development of the profile through weathering and translocation of clays (Dickson and Crocker 1953 cf. Stevens and Walker 1970). Since the time required for mature Podzols to form in the area is in the order of thousands of years (Howell 1978), only the first stage is seen on these young surfaces. There has not been enough time for weathering and illuviation of clays.

The major parent material is highly calcareous moraines with a minor aeolian component at the Icefield site (Walker et al. 1982b) (see Section 1.3.4). The high carbonates are a second major factor and from a clay genesis perspective are the overriding factor (D. Pluth pers. comm.). They impede soil genesis by slowing down the leaching (podzolization) process by retarding the translocation of clays (Howell and Harris 1978).

Climate, especially microclimate, also plays a major role in the rate and direction of soil development (Howell and Harris 1978) as is shown by the contrasting soil development conditions at the two study sites and the associated effect on vegetation development.

1.3.7.1 Methods

In these sites where the time frame is limited, most of the discernable soil changes are in profile development: morphological differences, texture, C/N ratio and organic and carbonate carbon. These should be studied rather than clay mineral formation and translocation which are the concerns of soil genesis studies over longer time periods (D. Pluth pers. comm.). The important soil properties in terms of plant growth are phosphorus, potassium, nitrates, ammonium, organic carbon and carbonates (Buckman and Brady 1969, p. 20), so the laboratory analysis concentrated on these.

Soils were not sampled at the Icefield site. At the Southeast Lyell Glacier, five soil pits were dug at random locations on both the terminal moraine and the most recent recessional moraine to determine rates of soil change over time. Due to time constraints, intermediate sites were not sampled. The soil profiles were described using criteria set by the Canadian Soil Survey Committee (1978a). Soil samples were collected from all horizons, then weighed, air-dried and sealed in the field. All laboratory chemical and mechanical analyses were conducted using the following methods described by the Canadian Soil Survey Committee (1978b).

Soil reaction (pH) was determined with a pH meter using a 0.01 M $CaCl_2$ 1:2 soil:solution ratio and a 1:2 soil:water ratio. Total nitrogen (ammonia included, nitrate and nitrite excluded) was determined with the macro-Kjeldahl method using a Kjeltec Autoanalyzer while exchangeable ammonium (NH_4^+) and nitrate (NO_3^-) was extracted using a 2N KCl solution, with analysis done on a Technicon Autoanalyzer II.

The total amount of carbon in each sample was found by dry combustion in a LECO induction furnace. Carbonate carbon was determined using the calcium carbonate equivalent pressure method with a mercury

manometer. Organic carbon was calculated indirectly using the difference between total and inorganic carbon.

Particle size distribution of the fine earth fraction (<2 mm) was determined using the Bouycouos hydrometer method, with no pretreatment to remove carbonates or organic matter prior to dispersion in a sodium hexaphosphate solution. For the calculations, results are expressed, where applicable, as a percentage of oven dry weight.

1.3.7.2 Southeast Lyell Glacier Site[5]

The rate of soil development at the Southeast Lyell site is similar to that reported for the Mount Robson moraines (Tisdale et al. 1966, Sondheim and Standish 1983, Blundon 1989). Both are calcareous sites with calcium carbonate equivalent ranging from 70-85% (Walker et al. 1982b, p. 510, Sondheim and Standish 1983). As with the studies by Crocker and Major (1955) and Crocker and Dickson (1957), the main gradients observed in the field are organic matter, reaction, bulk density and colour: physio-chemical or mineralogical changes are not apparent in the chronosequence. Table 1-11 is a profile description for a soil pit on the terminal moraine.

While carbonates and a short time interval since stabilization restrict soil development, this site has a relatively mild climate (see Section 1.3.3) so that vegetation is quickly established and forest growth is rapid (see Section 1.3.6). This results in perceptible changes in soil properties once vegetation is established. On surfaces less than 100 years old, the most obvious development is incorporation of the decomposing *Dryas* material into the surface mineral horizon, which is done by physical and mechanical means (Walker et al. 1982b, p. 510). Vegetation establishment and particularly litter buildup accelerates the

[5] Unless specified otherwise, the results described here are for the terminal moraine.

TABLE 1-11

SOIL PROFILE DESCRIPTION

SOUTHEAST LYELL GLACIER TERMINAL MORAINE

Site: Closed Picea engelmannii forest, moraine crest

Soil Classification: Orthic Regosol

Horizon	Depth (cm)	Description
FH	10-0	Black (10 YR 2/1 m), very dark brown (10 YR 2/2 d); abundant, very fine, fine and medium, random and horizontal roots; abrupt, smooth boundary; 8 to 15 cm thick.
Ahk	0-0.5	Very dark grayish brown (10 YR 3/2 m), dark grayish brown (10 YR 4/2 d); sandy loam; weak, fine, granular; very friable; abundant fine and plentiful, very fine, vertical and random roots; strongly calcareous; abrupt, smooth boundary; 0 to 1 cm thick; alkaline.
Bmk	0.5-2	Very dark grayish brown (10 YR 3/2 m); brown (10 YR 4/3 d), sandy loam; weak, fine, subangular blocky; very friable; plentiful, very fine and fine, and frequent medium, random roots; extremely calcareous; abrupt, smooth boundary; 0.5-3 cm thick; strongly alkaline.
BCk	2-5	Gray (10 YR 5/1 m), light brownish gray (10 YR 6/2 d); loam; very weak, fine, subangular blocky; very friable; plentiful, fine and few medium, vertical roots; extremely calcareous; stony; clear, smooth boundary; 0.5-4 cm thick; strongly alkaline.
Ck	5+	Gray (10 YR 5/1 m), light gray (10 YR 6/1 d); loam; amorphous; very friable; few, medium and fine vertical roots; extremely calcareous; stony; strongly alkaline.

leaching of soluble materials and exchangeable metal cations (Crocker and Major 1955).

The youngest soils had almost no development except the presence of a few roots (Walker et al. 1982b, p. 512). The oldest areas just inside the trimline have undergone some weathering of carbonates, as evidenced by an incipient B horizon, but are still regosolic (Walker et al. 1982b, p. 512).

The soil development on similar-aged surfaces varies greatly due to micro-topographic differences. Crocker and Major (1955) state that at Glacier Bay, early variations in soil properties result from heterogeneity of the colonizing vegetation, but that by the alder thicket stage (35 years), these variations have gone. At the Southeast Lyell site, the opposite appears true; differences in micro-site soil development are enhanced as time progresses. Substantial differences in the state of soil development were observed in sites only a few metres apart due to the complex mosaic of slope aspects and angles, texture, moisture and plant cover.

The development of an organic surface layer varies greatly with micro-topography, ranging from less than 1 cm on exposed hummock tops to 15 cm in shady inter-hummock depressions. In the latter case there is a trend toward Orthic Humic Regosols. Thin Ahk and Bmk horizons are present, although discontinuous, and are the initial phases in the development of a Brunisolic soil. However, their development is such that the soils are classified as Orthic Regosols. Average combined A (range 0-6 cm) and B (range 0-3 cm) horizon thickness was 5 cm which compares to 11 cm and 25 cm on similar-aged surfaces at Mount Robson, and Glacier Bay, respectively (Crocker and Major 1955, Tisdale et al. 1966).

Some of the steeper ($>10^0$), more exposed moraine crests are still bare of vegetation even after 100 years. Mass movement processes such as

small landslips and mudslides are common on these surfaces (Howell and Harris 1978) and result in poorly developed soil with little horizon differentiation.

All the soils are of the same parent material, and fall within the loam to sandy loam texture category. No differences in the clay and silt fraction between the 6 and 143 year-old surface were noted. Although this could be a result of the sampling and analytical techniques used, most other researchers do not find textural differences over a 200 year span (e.g., Crocker and Major 1955, Sondheim and Standish 1983). In cases where the silt fraction increases, it is attributed to aeolian deposits (Viereck 1970, Purchase and La Roi 1983). Studies on longer chronosequences (e.g., Chandler 1942) do find increases in both the silt and clay fraction over time.

Although profile development is weak, the A and B horizons on the terminal moraine have marked changes in chemical composition when compared to the material from the youngest moraine and the underlying C horizon (Table 1-12). Organic carbon and pH from a 50 year-old surface at the Southeast Lyell site (Walker et al. 1982b, p.510) are intermediate in value to samples from the recent and recessional moraines as shown in Table 1-12.

Only the overall rate can be determined, because soils were sampled from the two end points in the chronosequence; local trends over time cannot be inferred. However, changes in soil characteristics in these environments are probably unidirectional. For example, Sondheim and Standish (1983) conclude that on the Mount Robson Moraines, trends in soil properties such as percent organic carbon, percent total nitrogen, C/N ratio and pH are mostly unidirectional with age, and that parent material variability did not mask the overall trends.

Generally on these sites, accumulations of nitrogen and organic carbon and changes in pH are most pronounced in the upper horizons;

TABLE 1-12

CHEMICAL ANALYSIS OF SOILS FROM THE SOUTHEAST LYELL GLACIER SITE [1]

	Recent Recessional Moraine (6 years old)	Terminal Moraine (143 years old)			
Horizon	CK	LFH	Ahk	Bmk	Ck
Sample Size (n)	10	5	3	2	10
pH CaC12	6.9 (0.02)	6.04 (0.3)	6.9 (0.1)	6.6 (0.1)	7.0 (0.1)
pH water	8.3 (0.04)	6.9 (0.3)	7.7 (0.1)	7.6 (0.1)	8.2 (0.1)
Total N (%)	0.02 (0.001)	1.6 (0.1)	0.1 (0.0)	0.1 (0.02)	0.04(0.004)
Ammonium (ppm)	0.2 (0.01)	76.0 (29.3)	1.2 (0.1)	1.6 (0.3)	0.3 (0.1)
Nitrate (ppm)	0.0 (0.0)	0.4 (0.03)	0.6 (0.01)	0.5 (0.1)	0.6 (0.02)
Total Carbon (%)	8.3 0.1	43.9 (1.9)	12.7 (0.3)	11.2 (0.4)	9.3 (0.1)
Carbonate Carbon (%)	8.7 (0.1)	0.6 (0.2)	8.3 (0.3)	7.5 (0.6)	9.1 (0.1)
Organic Carbon (%)	0.0 (0.0)	43.2 (2.1)	4.3 (0.6)	3.8 (1.0)	0.3 (0.1)
Organic Matter (%)	0.0 (0.0)	74.4 (3.5)	7.4 (0.9)	6.4 (1.7)	0.4 (0.2)
Organic C /N Ratio	--	27:1	36:1	37:1	6:1
Conductivity (uV)	69.3 (1.4)	128.7 (13.1)	166.8 (18.5)	162.5 (12.2)	91.7 (4.1)

1 Based on analysis of samples taken from 5 soil pits on the recent recessional moraine and terminal moraine. All soils sampled were Orthic Regosols, with a sandy loam to loam texture.

Data are represented, where applicable, by the mean value, followed by the Standard Error of the Mean (in brackets). Values are not assumed to be normally distributed. Percent values refer to oven dry weight.

these changes extended downward through the solum with time (e.g., Crocker and Dickson 1957, Ugolini 1966, Sondheim and Standish 1983). Even on surfaces 200 years old, most of the nutrients are still concentrated within the upper 23 cm (Crocker and Major 1955).

At other calcareous sites, soil acidity increases rapidly after vegetation establishment, especially in the LFH and Ahk horizons, falling from 8.0 to 5.0 or less in 40 to 60 years (e.g., Jacobson and Birks 1980, Sondheim and Standish 1983). These changes in pH are controlled mainly by the production of acids associated with organic matter, rather than by carbonic acid production (Sondheim and Standish 1983) so are vegetation-dependant rather than time-dependant. Several researchers (Crocker and Dickson 1957, Fitter and Parsons 1987) support this by noting that pH is constant over time on plant-free surfaces. While the trends are similar, pH values at the Southeast Lyell site do not decline to values reported at Glacier Bay (Crocker and Major 1955), probably due to differences in vegetation development and precipitation amounts. Fairly low pH values were noted (4.8) in the thicker LFH horizon in hummock depressions on the terminal moraine. The pH in the upper solum decreases only slightly, however (Table 1-12). The pH values on the Southeast Lyell terminal moraine may decrease over time, because in these calcareous environments, soil properties cannot reach a steady state until the carbonates are depleted (Sondheim and Standish 1983).

The changes in nitrogen concentrations over time are often similar between many of these deglaciated environments (Jacobson and Birks 1980). Nitrogen accumulates at low levels on bare ground through surface absorption or fixation by algae (Crocker and Major 1955), although substantial increases are not noted until macroscopic vegetation develops. This early vegetation usually includes some nitrogen-fixing species (Stevens and Walker 1970). At the Southeast Lyell site they are *Dryas drummondii* and *Shepherdia canadensis*; other N-fixing species on deglaciated landscapes in the region include *Dryas octopetala*, *Hedysarum mackenzii* and *Alnus crispa*. Their role in N-fixation is well documented

and includes circumstantial (ectomycorrhizal sheaths, mycorrhizal root nodules) and direct evidence (Lawrence 1953, Gardener and Bond 1957, Schoenike 1957, Lawrence 1958, Sprague and Lawrence 1960, Lawrence et al. 1967, Wilson 1978).

The highest rate of increase and the maximum concentration of nitrogen corresponds to the period when N-fixing species are highest in cover (Crocker and Major 1955, Crocker and Dickson 1957). Within several years after establishment, *Dryas drummondii* begins to fix significant amounts of atmospheric nitrogen. In southwestern Alberta, Wilson (1978) observed root nodules on four-year-old plants and an overall annual nitrogen fixation rate of 0.8-4.2 g/m^2. Initially, the nitrogen is mostly incorporated by the plant (Fitter and Parsons 1987), but later is released to the soil. Although *Dryas* can initiate nitrogen buildup in the litter and mineral soil horizons, *Alnus crispa* is much more effective. At Glacier Bay, litter and soil nitrogen concentrations under *Alnus* were twice that of *Dryas* for 20 year-old surfaces (Crocker and Major 1955), and in the alder stage, nitrogen accumulates rapidly. Where the two species co-occur, *Alnus crispa* plays a much more important role in enlarging the nitrogen pool and in stimulating growth of adjacent shrubs (Schoenike 1957, Lawrence et al. 1967). Alnus spp. are not present at the Southeast Lyell site. *Shepherdia canadensis* has N-fixing root nodules (Gardener and Bond 1957) and may play a similar ecological role at the Southeast Lyell site as *Alnus* does elsewhere. Nitrogen concentrations in the litter and Ahk horizons on the terminal moraine at Southeast Lyell are comparable to those at Glacier Bay under *Dryas* (Crocker and Major 1955).

On older surfaces when *Dryas* spp. and shrub species are replaced by *Picea* spp., nitrogen accumulates at a reduced rate (Crocker and Dickson 1957) or is actually depleted in the upper horizons (Crocker and Major 1955, Ugolini 1968, Sondheim and Standish 1983). This is due to increased nutrient uptake by later non N-fixing successional species (Sondheim and Standish 1983), with circumstantial evidence by the large

number of *Abies* roots in the lower organic horizons seen both at the study site and Glacier Bay (Crocker and Major 1955). Apparently, upper horizon N concentrations eventually approach a steady state (110 years reported by Crocker and Major (1955)).

The initial carbonate value of 8.3% for age 6 at the Southeast Lyell site moraine is similar to that at the Glacier Bay site, which start at around 5% and fall to less than 1% in 30 years (Crocker and Dickson 1955). The rate of calcium carbonate ($CaCo_3$) leaching is mostly dependant on the thickness of the surface organic layer and amount of precipitation. Decreases in calcium carbonate are most rapid under *Alnus crispa* and other shrubs which trap organic matter (Crocker and Major 1955) and less rapid under *Dryas* spp.

At the Mount Robson moraines, organic carbon content and C/N ratio increases with age and decreases with depth (Sondheim and Standish 1983); results from the Southeast Lyell site agree. There has not been much time for soil mixing to occur, as indicated by the relatively low organic carbon concentrations in the Ah horizon (Table 1-12). The C/N ratios at Glacier Bay are 13-15 under *Alnus* (Crocker and Major 1955). Under *Abies* on older surfaces, N depletion increases the ratio to 20-24 in mineral soil and 30 in the LFH horizon; similar values are found at the Southeast Lyell terminal moraine. Usually, organic carbon, nitrogen and pH are strongly related. The first two are inversely related to pH. Increases in these values are due to vegetation development and associated microbial activity (Sondheim and Standish 1983). Nitrogen produced by symbiotic fixation and other mechanisms quickly attains equilibrium with respect to organic carbon (Sondheim and Standish 1983).

Cation exchange capacity increases with clay and organic matter content (Howell and Harris 1978, Chandler 1942). Soluble salt concentrations on the terminal moraine are in the .082 to .200 mV range (82-200 uV) which are considered as low soluble salts (D. Pluth pers. comm.).

Based on ecological classification maps, the soils in the adjacent old-growth valley bottom *Picea-Abies* forest are Eutric Brunisols (BV3) (McEwen et al. 1982a). Soils of this type are formed on calcareous, coarse-textured glaciofluvial deposits in the lower subalpine (Walker et al. 1982b, p. 210) under *Picea-Abies*/feathermoss forests (C14 vegetation type) on gentle grades. The major factors are long term landform stability and consistent parent materials. The 143 year-old moraines at this site represent only the earliest phases in the development toward this soil type.

Soils developed on the valley slopes are mapped as a Brunisol-Podzol complex (BY1) (McEwen et al. 1982a). The dominant Eutric Brunisols are developed on calcareous, medium-textured morainal blankets materials and medium acid to mildly alkaline (pH > 5.5) B horizon (Walker et al. 1982b, p. 213). They are intermixed with subdominant Orthic Humo-Ferric Podzols which are confined to moist cool environments, usually on aeolian deposits.

Due to the complex topography within the trimline, the steady state soils will probably be a combination of the valley bottom and valley slope soil types described above. As well, gleysols can be expected in some of the silty closed depressions found within the trimline.

The time interval required to reach steady state on these surfaces is in question. In terms of nitrogen, carbon and other macro-nutrients important to plant growth, it is reached in less than 200 years on the Mount Robson moraines (Sondheim and Standish 1983) and Southeast Alaska (Crocker and Major 1955). However, these young soils cannot be considered to be in a true steady state, because at this time there has not been a significant depletion of carbonates from the upper horizon (Sondheim and Standish 1983). Other studies indicate that an apparent steady state of total N is probably temporary on 200-year-old surfaces, as shown by a comparison with higher nitrogen levels on adjacent older surfaces (Crocker and Dickson 1957).

When clay development is considered, the time frame is much longer. Mature podzols in the area have formed within the last 8500 years (Harris and Howell 1977 cf. Howell and Harris 1978). This is still a much longer time period than Podzol formation in coastal Alaska, which is estimated at 1000 years by Chandler (1942). Many researchers suggest that soils may actually deteriorate and end in paludification as internal drainage of soils deteriorates during podzolization (Jacobson and Birks 1980).

In summary, soils formation at the Southeast Lyell site lags behind the vegetation development. They are still regosolic, with incipient brunisolic qualities. Their genesis will be retarded until the carbonates are removed form the upper solum.

1.3.7.3 Columbia Icefield Site

The soils at the Icefield sites do not have a consistent age gradient (from present river channel to edge of outwash surface) because of the more random process of stream channel abandonment (see Section 1.3.5). At this upper subalpine site, the macro- and meso-climatic influence in retarding soil development is more pronounced (higher winds and lower temperatures) (Howell and Harris 1978). Although stabilized for over 100 years, the oldest surfaces at the Icefield site had almost no soil development, perhaps partly due to the cyclical vegetation development (see Section 1.3.8). Unlike the Southeast Lyell site, the Icefield site was not subject to slope processes, but the more severe climate results in other processes which restrict soil development.

On the coarse-textured glaciofluvial floodplain the soils are rapidly- to well-drained, highly-calcareous Orthic Regosols. (Walker et al. 1982b, p. 390). Mottling is rare, even where the water table is high, because the soils are cold, poor in organic matter, and

calcareous, all of which provide a poor environment for microbial reduction (Walker et al. 1982b, 391). As well, rapid surface and internal drainage prevent long periods of saturation.

Low temperatures result in dominance of physical weathering while frost activity can mix soils and disrupt profile continuity (Howell and Harris 1978). The short growing season limits plant growth and this along with the coarse-textured calcareous rock inhibits the organic breakdown of the parent material through microbial and chemical action (Laycock 1957 cf. Howell and Harris 1978).

Winds affect soil development through desiccation and transport (Howell and Harris 1978). The first condition causes dry conditions and retards chemical weathering. Strong winds can limit the depth of A and B horizons resulting in immature soils in exposed locations (Pettapiece 1971 cf. Howell and Harris 1978), which is the case at the Icefield site.

Most importantly, climatic conditions restrict vegetation development. Vegetation is needed to stabilize the surface, trap wind-blown material, accelerate chemical and microbial processes and build up the nutrient pool. Under *Dryas* clones, aeolian deposits up to 3 cm thick were noted. On surfaces where the *Dryas* clones were decaying, as the surface became re-exposed, any accumulated surface fines were removed, and the surface appeared to be fresh unaltered material. Until stabilized vegetation is established, the soil development will probably be severely restricted.

The rate of pH decline under *Dryas* is slower at this site than reported for Glacier Bay, probably due to the slower rate of vegetation development (Fitter and Parsons 1987).

In examining foliar and soil nutrient levels on the Athabasca Glacier moraines, Fitter and Parsons (1987) concluded that nitrogen and

phosphorus cycles are initiated even in these low productivity sites as indicated by higher concentrations of these elements under *Dryas* clones. They believe that N fixation does not occur by root nodules as none were seen in their study. They contended, rather, that N accumulation was due to fixation by free-living microbial organisms as evidenced by the abundance of ectomycorrhizal root sheaths. During the field season, however, large, fleshy root nodules on *Dryas drummondii*, similar to those found by Tisdale et al. (1966) and Schoenike (1957), were observed on several clones at the Columbia Icefield. Since these nodules usually develop at dept greater than 15 cm (Lawrence et al. 1967) and only root crowns of *Dryas* were collected for surface age determination, they may be much more common, as reported by Wilson (1978). In any case, N fixation probably occurs both by root nodules and ectomycorrhizal root sheaths in this environment.

If conditions allow vegetation to become permanently established and the soils to become well developed, they may become Orthic or Eluviated Eutric Brunisols. These are the soil types occurring on adjacent valley slopes (McEwen et al. 1982b) on morainal blankets composed of calcareous medium-textured till, overlying inclined bedrock.

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2 PLANT PATTERN DEVELOPMENT DURING PRIMARY SUCCESSION ON PROGLACIAL DEPOSITS IN THE CANADIAN ROCKY MOUNTAINS

2.1 Introduction

Investigation of the changes in "spatial pattern" of plants (defined as a departure from a random distribution of species) during the course of succession has preoccupied some ecologists for many years (Mead 1974), especially since Watt (1947a) articulated many of the important concepts. Since then, there have been a number of review papers on the ecological significance of plant pattern (Hopkins 1957, Greig-Smith and Kershaw 1958, Kershaw 1963, Greig-Smith 1979, White 1979). The classic view has been that spatial pattern over a small area is mostly due to plant morphology and sociological effects (Hill 1973), in which case the pattern is largely autogenically controlled. Some studies have pointed out the major effect that environmental heterogeneity can have on obscuring species pattern (and contributing to it) even over a small distance (Veblen and Ashton 1979). This latter viewpoint emphasizes the allogenic controls on pattern. This plant pattern is distinguished from the more general concept of "vegetation pattern". This latter term refers to a large-scale association between vegetation and certain environmental variables. It is not always based on quantitative methods, unlike plant pattern analysis.

Pattern analysis in ecology may be approached from two different viewpoints. First, pattern may be examined in relation to causes: underlying heterogeneity of the environment, processes by which colonization and vegetation development occur, and the spatial effects of senescence and competition. Second, pattern may be viewed in terms of its effects on interactions in the existing plant community, on further community development, and on the associated animal community.

2.1.1 Spatial Pattern Characteristics

"Spatial pattern", in a mathematical context, can be defined as non-random heterogeneity, with a certain periodicity (Dale and MacIsaac 1989). In an ecological context, it can refer to spatial variation in the density of a species or species group (Pielou 1974). This can be examined with respect to some environmental factor. Pattern can be studied at a single species level, or using groups of species based on characteristics such as growth or life form.

Plant pattern can be considered to consist of two phases: "patches" and "gaps" (Pielou 1977). As well, two parameters of plant pattern can be recognized: "scale" and "intensity". Although these terms are most applicable when the species or vegetation is overdispersed (clumped or contagious), they can also be applied in cases of underdispersion (regular or uniform). In the ecological literature, these terms are rarely defined explicitly and there has been confusion as to their exact meaning, especially with pattern intensity (Kershaw 1970, Hill 1973).

"Patch size" can be defined as the average size of the plant cover patches in a mosaic of patches and gaps. In pattern studies, patch size is also defined and delimited as areas where species cover is greater than an arbitrary threshold density. Patch size has also been referred to as "scale" or "grain" by some authors (e.g., Hill 1973, Pielou 1977). When the formulas used to detect this patch size are examined closely, it is apparent that what they are referring to is actually pattern scale (defined below) (see Galiano 1983). "Gap size" is the average distance between the perimeters of patches. It can be areas where the species or species group in question is totally absent, or where it occurs at a density lower than the threshold density.

Patch size and gap size combine to create pattern scale. "Scale" can be defined as the average distance between the centre of the patch and the centre of the gap. Conversely, it can be defined as one-half the sum

of the average patch and gap size (Usher 1975) (Figure 2-1). Pattern scale has also been referred to as "grain" by some authors (e.g., Pielou 1974, 1977).

"Pattern intensity" is the variation in a species' density over distance and can be defined as the degree of contrast between the density of plants in the patches and the gaps. Pielou (1977) states that pattern intensity is independent of patch size or pattern scale, but Hill (1973) doesn't agree. Figure 2-1 gives three examples of how the components of spatial pattern in vegetation might change over time to clarify the terms as defined above.

Figure 2-2 illustrates four characteristics of spatial pattern. Uninterrupted pattern occurs where the primary (smallest) scale of pattern occurs without a break, whereas, with interrupted pattern, the primary pattern is only present intermittently over distance. The latter situation results in a secondary level of scale, with the "patches" being the areas where the primary pattern is present. Regular pattern is characterized by patches and gaps which are constant over distance, while balanced pattern occurs when the patch and gap sizes are equal. In situations where the plant density drops or rises sharply, the patches/gaps have a sharp boundary; in cases where density changes over a wider distance, the boundary is smooth.

In the simplest cases of spatial pattern, there is only one scale. In most ecological examples, however, there are two or more scales. Multiple scales are additive, with the overall scale a combination of larger (secondary) pattern superimposed on the smaller (primary) scale pattern. In this context, small scale means that the patch and gap sequence is repeated over a small distance, whereas larger scale patterns have larger patch and/or gap sizes.

Hill (1973) and Kershaw (1973) classify the underlying causes of pattern scale into three main types: morphological, sociological and

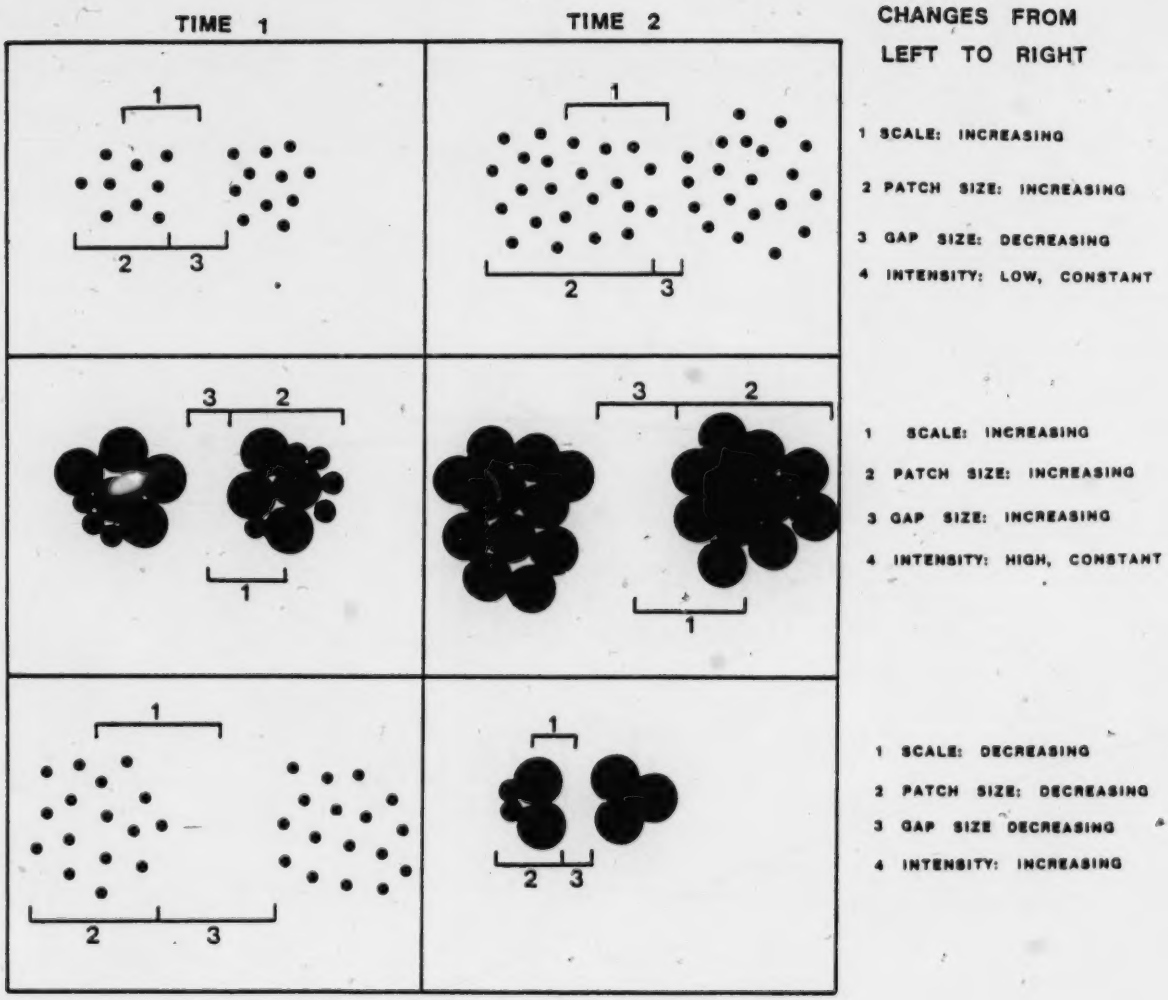
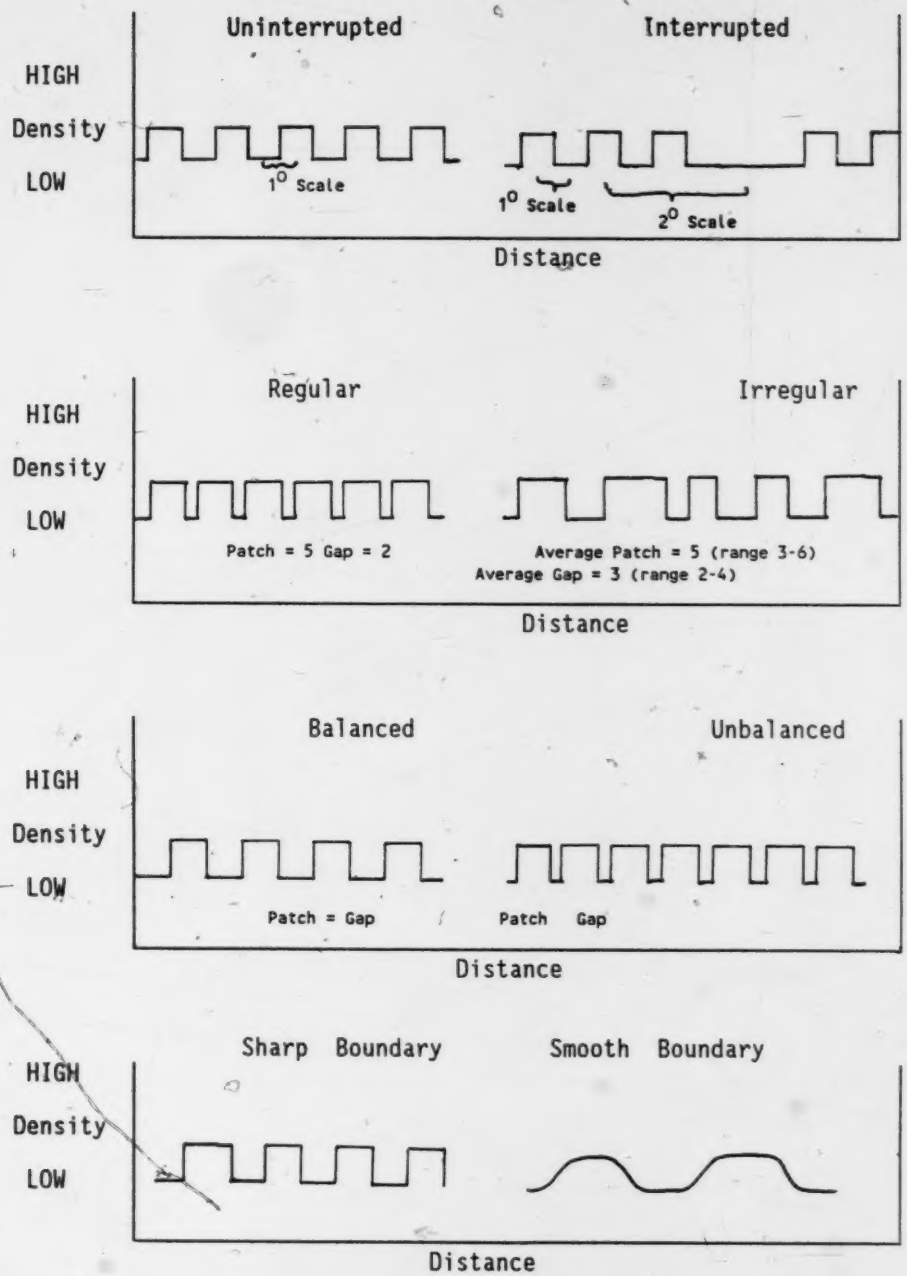


Figure 2-1 Components of Pattern: Scale, Intensity and Patch/Gap Size

Figure 2-2 Characteristics of Pattern



Source: Mark Dale, pers comm

environmental (ecological). In vegetation with several scales of pattern, each scale may be mostly due to one underlying cause. Small-scale pattern is often morphologically imposed and corresponds to the growth of the individual plants. At this small scale, the major factors influencing the pattern are processes of initial colonization and subsequent development of vegetation. Environmentally-imposed pattern is usually evident at larger scales and is the direct result of vegetation response to underlying environmental variation. Sociologically imposed pattern is due to the spatial effects of interaction (e.g., competition, senescence) between plant individuals and between plants and animals (Van der Maarel 1984). It often is the major underlying cause of intermediate levels of pattern. Notwithstanding the above comments, these underlying causal mechanisms often do not influence pattern scale at only one level. For example, Greig-Smith (1979) notes that slight variations in soil conditions can result in environmental pattern at a scale of only a few centimetres.

Most studies of pattern deal with species individually and/or in relation to selected environmental factors (Greig-Smith 1964, Usher 1975, Galiano 1982b). Other studies look at multi-species pattern using pattern analysis with multivariate analysis such as reciprocal averaging (Bouxin and Gautier 1982, Galiano 1983).

2.1.2 Pattern Development During Primary Succession

In 1964, Greig-Smith presented a model to predict changes in the pattern of vegetation undergoing succession. This model is based on the following premises: (a) The pattern of vegetation is determined by the pattern of species composing it. (b) The pattern exhibited by each species at any point in time is a result of the species morphology and tolerance to the prevailing environmental conditions, including the effect of other organisms.

This model states that during any successional sequence, there is a predictable sequence of pattern development. It predicts that each species will pass through several stages of successively larger patch sizes and lesser intensities of pattern corresponding to the establishment, growth and coalescence of patches of the species. Pattern scale is initially determined by the grain of the environment which controls the spatial distribution of "safe sites" for establishment of colonizing individuals (Harper 1977, p. 112). As long as there is not subsequent recruitment, the scale of pattern stays the same, until the individual initial patches (or individuals) coalesce, although the patch size will reach a maximum while conditions are optimal for growth of that species. Pattern intensity will initially increase as the succession proceeds, and then, as Brereton (1971) notes, it will decrease rapidly as individual plants coalesce to form large patches. At this point, the smallest scale of pattern disappears. If the species attains ubiquitous distribution even the larger scale environmental pattern will disappear. If the environment changes beyond the tolerance of the species, the patches start to break up, at which time the sequence of events noted above reverses. Patch size will decrease while the scale of pattern will remain unchanged or start to decline. The intensity of the pattern will increase initially and then decline. Pattern will eventually become more irregular, due to death of individuals and breakup of patches, eventually ending in the species disappearance from the community. This reduction in patchiness has also been noted by Mack and Harper (1977). In summary, the early seral vegetation is composed of small-scale patterns of high intensity, while in the latter stages, there are larger-scale patterns of low intensity.

Yarranton and Morrison (1974) examined the development of vegetation during primary succession on sand dunes. They found that Greig-Smith's model was supported, but concluded that the sequence of spatial pattern changes may be repeated for each stage in a long-term succession. Their "theory of nucleation" suggests that just as dust particles act as condensation nuclei for rain drops, in primary succession, the

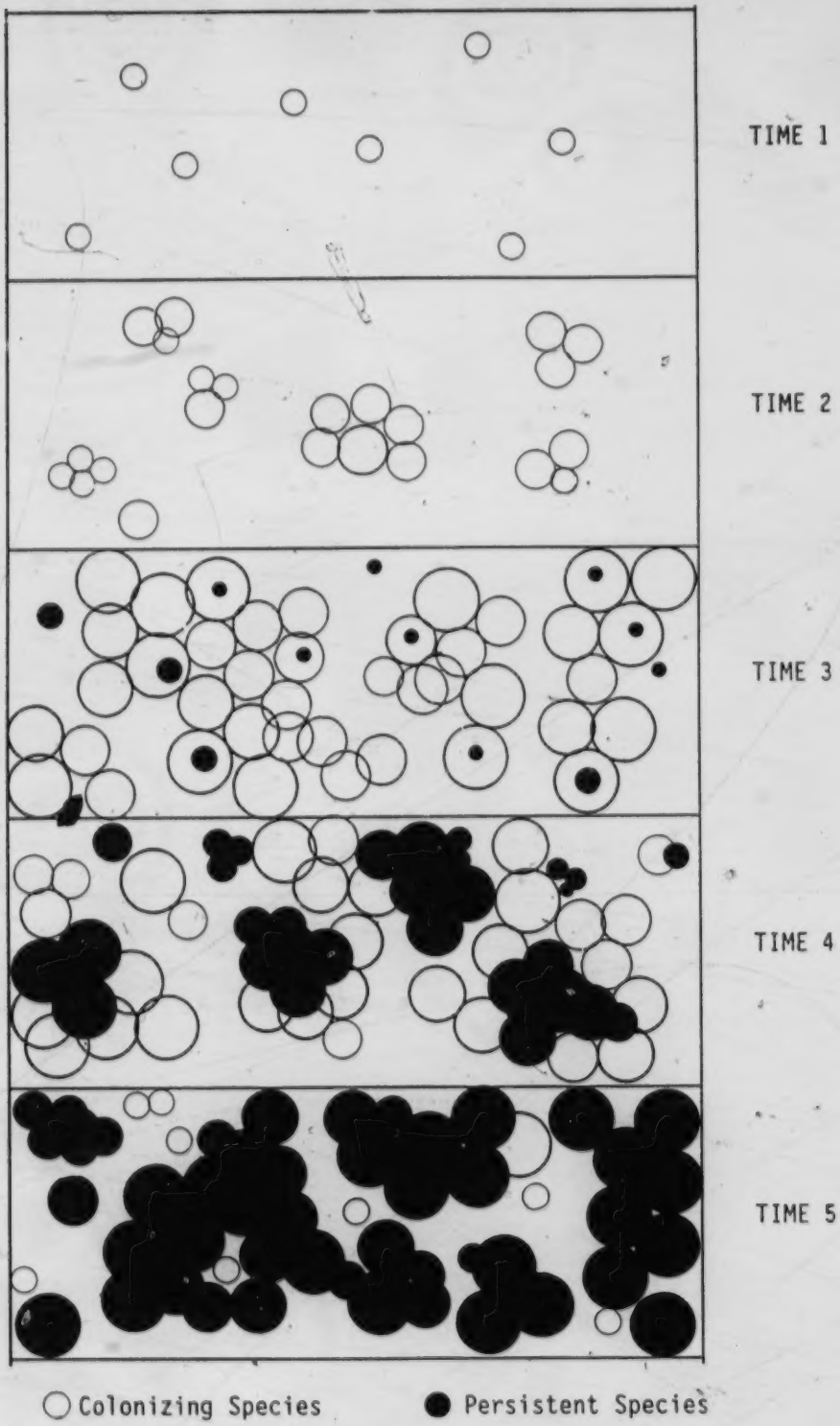
"colonizing" species may act as nuclei for the recruitment of the "persistent" species. This occurs when the colonizers are needed to modify the micro-environment making it more suitable for the later species, and corresponds to the facilitation model reviewed by Connell and Slatyer (1977). The patch size will increase as clumps of a given species group are established, grow and coalesce, and then decrease as the group is replaced by another.

This nucleation phenomenon has been observed for various species in primary and secondary successions: *Juniperus virginiana* and *Quercus prinoides* in sand dune succession (Yarranton and Morrison 1974); *Juniperus virginiana* and *Taxus baccata* in secondary old field succession (Kirby 1977); *Alnus* spp. and *Dryas drummondii* in primary and secondary succession at Glacier Bay, Alaska (Lawrence 1958); rainforest species invading savanna ecosystems in Central America (M. Kellman pers. comm.). Viereck (1970) noted that succession on glaciofluvial outwash in central Alaska is cyclic and follows a similar pattern development for colonizing and persistent species, in which patches of herbaceous vegetation are replaced by patches of shrubby species.

A hypothetical two-stage pattern development model, which corresponds to Yarranton and Morrison's thesis, is outlined below and summarized graphically in Figure 2-3. In primary succession, the early succession species can be classified as either "colonizing" or "persistent" species. Initially, the colonizing species exhibit low intensity pattern, small patch size and a scale determined by initial spacing of seedlings (Time 1, Figure 2-3). As they grow and coalesce (Time 2 and 3), patch size will increase, intensity will increase and then decrease, and the smallest scale of pattern will disappear.

In this model, persistent species tend to germinate in the centres of the existing patches of colonizing plants, because that is where the substrate is most modified for favourable establishment. As the persistent species grow and mature, they replace the colonizers (through

Figure 2-3 Hypothetical Two-Stage Pattern Development



competition or alteration of microenvironment). It is at this transition point (when the colonizing and persistent species are co-existent) that the community pattern is most complex (Time 4, Figure 2-3). As the colonizer species continue to senesce, their pattern development is reversed (intensity increases initially as patches decay, then decreases; patch size decreases; small scale pattern reappears). As the persistent species form larger and larger patches, their pattern development repeats that observed for the earlier seral stage.

This dynamic variation in vegetation pattern, which is repeated for every stage in the successional sequence, is based on the premise that the initial colonizing species act as nuclei for the recruitment of the later persistent species. Examination of this pattern can give insight into the mechanisms of succession (Yarranton and Morrison 1974).

I hypothesize that this cyclical sequence in species pattern development and nucleation mechanism is occurring on the glacial and proglacial deposits at the Southeast Lyell and Icefield study sites. The early colonizing species is *Dryas drummondii*, whereas the persistent species include *Abies lasiocarpa*, *Picea engelmannii*, and *Salix glauca* var. *villosa*[1]. Seeds of conifers and persistent shrub species (e.g., *S. glauca*, *Shepherdia canadensis*) tend to germinate within the decaying centres of the *Dryas* mats (Heusser 1956) and as they grow and mature, they shade out the *Dryas* (Wilson 1978).

2.1.3 Research Objective and Hypotheses

The major objective of this research was to determine the changes in pattern components (scale, intensity and patch/gap size) during primary succession on glacial moraines and outwash surfaces of known ages at two locations in the Canadian Rocky Mountains.

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[1] Future reference to species which are the only representatives in their genus may be by generic name only.

The hypotheses tested are as follows:

1. Nucleation hypothesis

   Clones of *Dryas drummondii* act as centres of nucleation for subsequent recruitment of conifer and shrub species.

2. Pattern Hypothesis

   The development of species pattern (scale, intensity, patch/gap size) during primary succession in proglacial environments follows the course outlined by Greig-Smith (1964). This development is repeated for both the colonizing (*Dryas drummondii*) and persistent (conifers, shrubs and non-vascular) species groups.

   The following predictions apply to all species groups:

   a) The smallest scale of pattern remains constant until the patches coalesce, at which time it disappears.

   b) The patch size is largest just after the species coalesce.

   c) Pattern intensity is at a maximum just before the patches coalesce, and has a second peak during the senescence phase as patches break up.

2.2 Methods

The study of autogenic *versus* allogenic pattern in plant communities can be approached using two different methodologies. When studying allogenic pattern, in which differences in the local environment are to be correlated with differences in vegetation, long transects with low sampling intensity are adequate (Maher 1971). However, the research discussed here is more concerned with autogenic pattern, caused by plant community development during succession. The best approach in studying autogenic pattern is to sample intensively over smaller areas (Veblen and Ashton 1979). Intensive, systematic sampling forces the investigator to look at the vegetation in detail, and focuses attention on small--scale patterns. The intensive method was used in this research.

Field work was conducted from June 30th to August 10th, 1984 at the Southeast Lyell site, and from August 13th to September 7th, 1984, at the Columbia Icefield site.

2.2.1 Field Methods: Nucleation

At the Southeast Lyell site, six areas where the cover of *Dryas drummondii* was discontinuous were chosen for nucleation sampling. The approximate surface ages and distances from the 1984 glacier terminus were as follows: Areas 1 to 4: 45 years old, 1100 m ; Area 5: 25 years old, 80 m ; Area 6: 40 years old, 600 m (Figure 2-4).

At each site, between 66 and 250 randomly-placed 1 m^2 quadrats were surveyed. In each quadrat, the percent cover of live *Dryas drummondii*, dead *D. drummondii* and bare ground was estimated separately. (Bare ground was defined as areas lacking non-vascular, herb or dwarf shrub species cover.) Bare ground was split into two groups by soil particle size: fines, gravel and cobbles; stones and bedrock. Within each cover type, the number of conifer or shrub saplings (of all heights) was

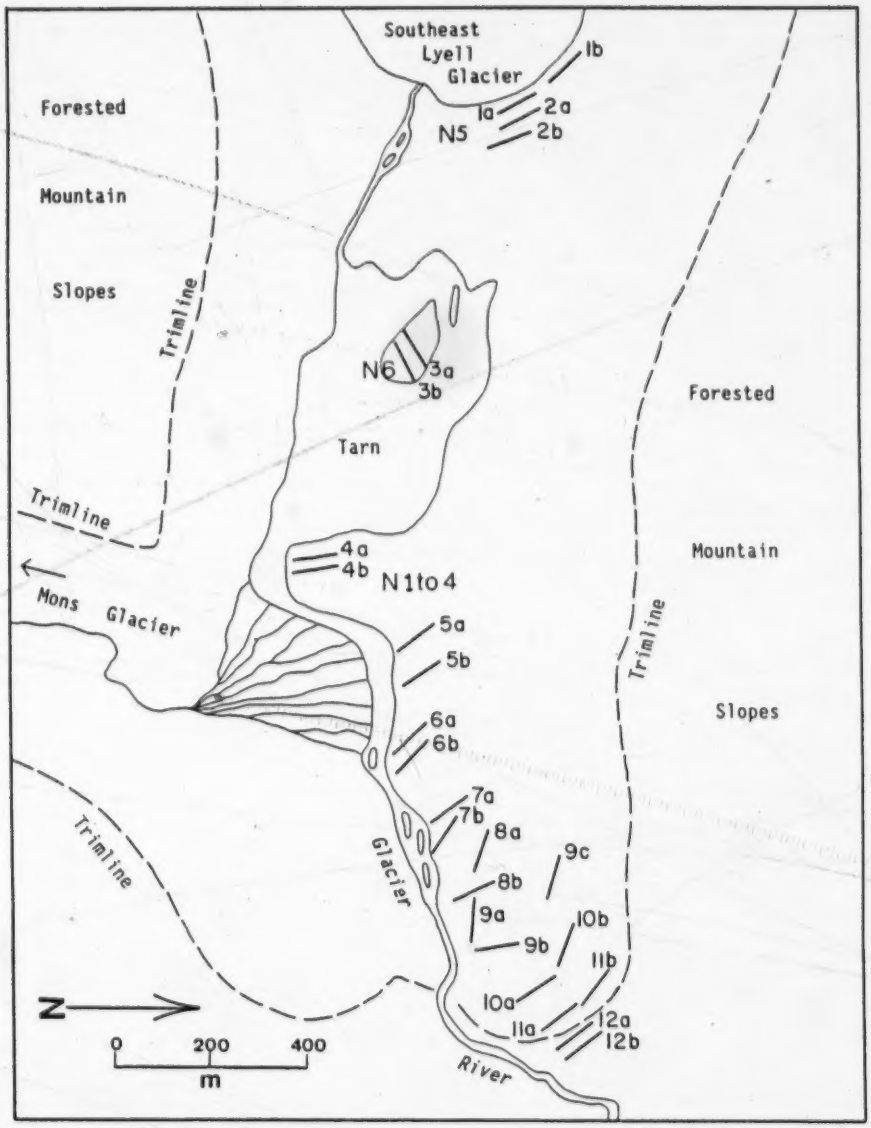

Figure 2-4 Location of Transects at the Southeast Lyell Glacier Site

N - Nucleation Site —— Pattern Transect

recorded. Nucleation was not tested at the Icefield site because of very low woody species densities.

2.2.2 Field Methods: Pattern Development

At the Southeast Lyell site, spatial plant pattern was sampled at 11 locations along a chronosequence, from 6 years on the most recent recessional moraine to 143 years on the terminal moraine and in the old-growth forest (>432 years old) just beyond the terminal moraine. In each location, two transects were sampled (Figure 2-4); close to the valley centre where possible. Each transect consisted of 300 contiguous 0.3 m x 0.3 m quadrats (90 m long). To control for site variability, the transects were located on gentle to moderate south- to southwest-facing mid-slope to lower-slope positions, on stable moraines. Within these constraints, the starting position of each transect was randomly situated, with the alignment approximately parallel to the moraine crests. Although most were in a straight line, several on the older surfaces were deflected a few degrees to remain on the moraine.

Within each contiguous quadrat in the transect, the percent "crown cover" for each macroscopic plant species (excluding non-vascular epiphytes and hornworts) was estimated[2]. Crown cover was determined by estimating the vertical projection of the ground area covered by a plant, disregarding openings in the foliage (Daubenmeir 1959). For species with a canopy over 5 m in height, a clinometer was used to determine if the foliage overlapped the quadrat.

To determine if there was ongoing recruitment of trees and shrubs or if there was just one cohort for each surface age, an estimate of the height-class distribution along each transect was made. This was done by estimating the cover for each woody species in each of the following

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[2]The term "crown cover" is used rather than "canopy cover" because of the various growth forms sampled.

strata: 0 - 0.5 m (dwarf-low shrub), 0.5 - 2.0 m (medium shrub); 2.0 - 5.0 m (tall shrub) and > 5.0 m (tree). A stratified random sampling method was used (Mueller-Dombois and Ellenberg 1974). Within each 30 m segment along each transect, a randomly-placed nested quadrat was used to estimate species covers in these upper strata. The following quadrat sizes were used: 2 x 2 m, 5 x 5 m and 6 x 6 m for the medium shrub, tall shrub and tree strata, respectively. The 5 x 5 m plot was nested in a randomly-chosen corner of the 6 x 6 m plot. A 2 x 2 m plot was nested in each of the four corners of the 5 x 5 m plot (four 2 x 2 m plots in total). Cover in the dwarf-low shrub layer was estimated in the quadrats used for pattern analysis.

At the Columbia Icefield, 10 transects were sampled at the Dome Glacier site and 10 transects were sampled at the Sunwapta River site. At the former site, the transects were aligned parallel to the Dome Glacier meltwater stream, while at the latter, they were aligned parallel to the Sunwapta River. The starting positions of the transects were randomly located and consisted of 300 0.3 x 0.3 m contiguous quadrats. They were situated along the two chronosequences such that all surface ages were sampled at least once (Figures 2-5 and 2-6). Within each quadrat, the percent "crown cover" of live *Dryas drummondii* and dead *D. drummondii* was estimated separately.

2.2.3 Methods of Data Analysis: Nucleation

The data collected to test the nucleation hypothesis were quadrat-oriented rather than stem-oriented. For this reason, only simple statistical analysis was possible in which the following question was answered: Is the stem distribution on each ground cover type different than that expected by random positioning?

This question was answered using a single-classification goodness of fit test. In this analysis, the G-test (Log-Likelihood Ratio Test) was

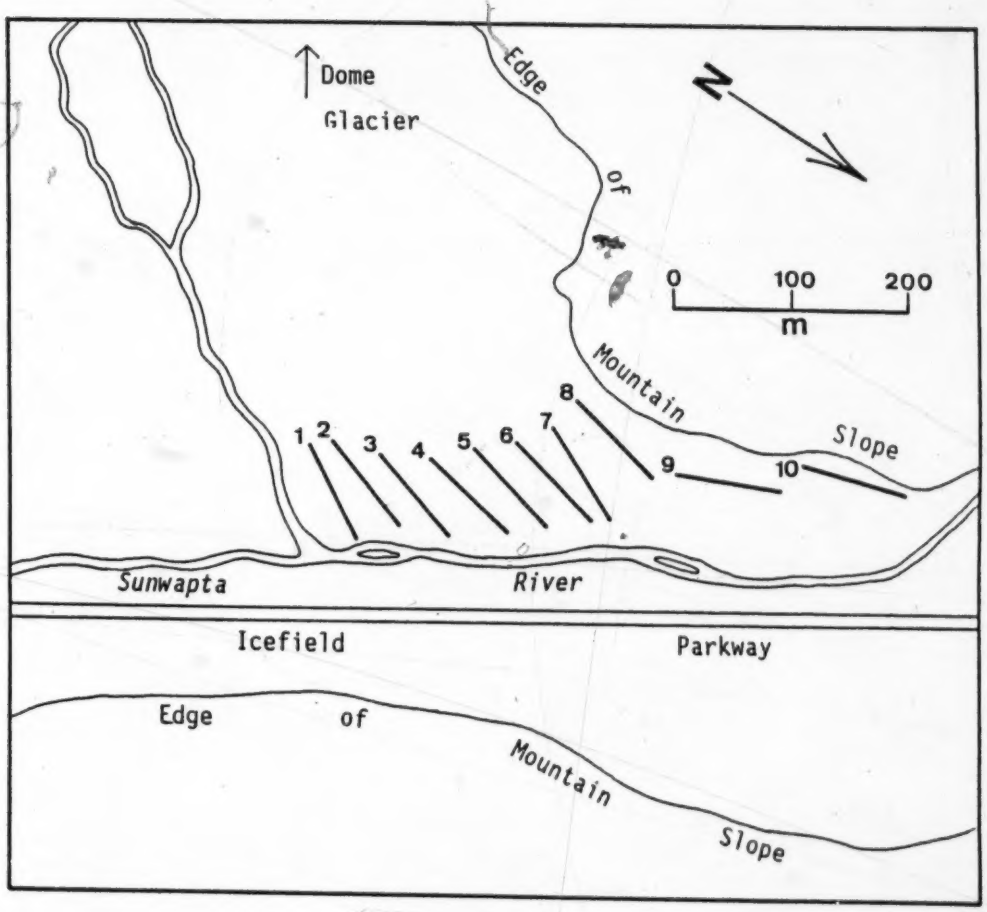


Figure 2-5 Location of Transects at the Dome Glacier Site

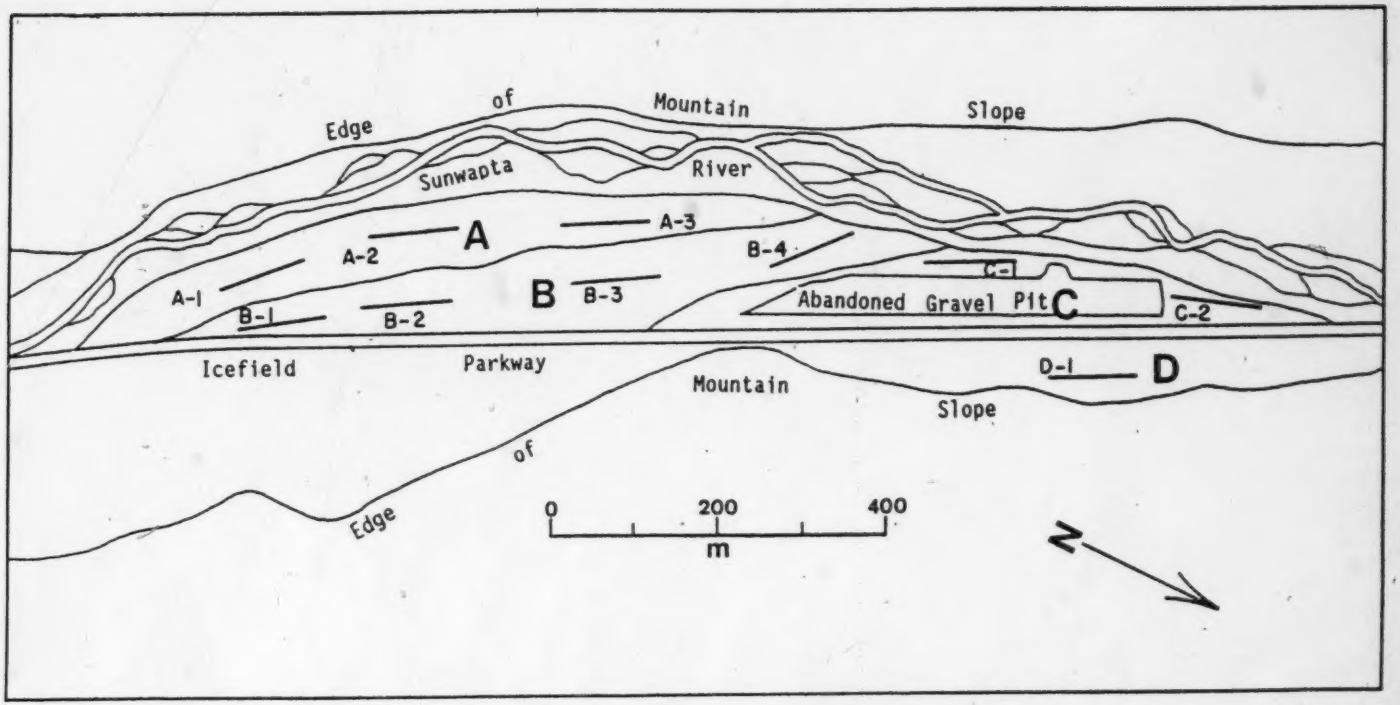


Figure 2-6 Location of Transects at the Sunwapta River Site

LEGEND

A,B,C,D Terrace Surface

performed with William's Correction. The null hypothesis was that the proportion of stems in each cover type (live *Dryas*, dead *Dryas*, and bare ground) was proportional to the area covered by each. The alternative hypothesis was that the proportion of stems in each cover type was not proportional to the area covered by each.

2.2.4 Methods of Analysis: Pattern Development

The pattern analysis was based on growth form "species groups" which were defined as follows: non-vascular - mosses, liverworts, lichens; shrubs - all shrub species (excluding *Dryas drummondii*); conifers: *Abies lasiocarpa* and *Picea engelmannii*. As *Dryas drummondii* is dominant at both study sites, it was also examined, as a separate "group".

Before the pattern components were analyzed, a "runs" test (Pielou 1977, p. 229) was performed on each species group along each transect to determine if they were distributed randomly or segregated into patches and gaps. This test labels each quadrat along the transect as "dense" or "sparse", using the median cover value as the criterion. Each uninterrupted series of dense or sparse quadrats is designated as one run. The number of observed runs is compared to the expected number (using a normal approximation) given the number of dense and sparse quadrats (Sokal and Rohlf 1981, p. 783). If the number is significantly less than expected ($P < .05$), then the species groups are concluded to be composed of patches and gaps.

Pattern analysis techniques are more complicated, and require a brief overview (as follows). The quantitative study of plant pattern can be traced to the 1920's (Greig-Smith 1964). The earlier studies most often focused on detecting plant dispersion (i.e,. random, overdispersed, underdispersed) and a wide variety of tests have been developed for this purpose (e.g., Pielou 1959). For a quantitative description of non-random pattern (including all its components), more sophisticated approaches were needed (Ludwig and Goodall 1978).

Generally, these latter methods of analyzing pattern can be divided into two groups: those that use plant-to-plant or point-to-plant distances and those based on data from individual or contiguous quadrats (Mead 1974, Carpenter and Chaney 1983). The latter category can be categorized as "square wave spectral analysis" methods (Ripley 1978) and include the most commonly used procedures of pattern analysis (Goodall 1974).

The first attempt at quantifying species pattern using contiguous methods was by Greig-Smith (1952 cf. Gibson and Greig-Smith 1986), using an analysis of variance technique on a grid of transects. This was later modified by Kershaw (1957) to a linear transect. Greig-Smith's original blocked quadrat variance (BQV) method and later modifications (e.g., Usher 1969) have been among the most widely used methods of pattern analysis (Yarranton 1969, Zahl 1977). There are, however, some drawbacks to this method which have been noted by Pielou (1977) and others.

The BQV method calculates the mean square of cover (density) for a block size of r quadrats within $2r$ quadrats. The block sizes are incremented by $2n$ (where n is the total number of quadrats), at each step, up to $n/2$. The blocks do not overlap at any one step.

The more recent Two-Term Local Quadrat Variance Method (TTLQV) of Hill (1973) is used in this research. It is similar to, but better than, Greig-Smith's Blocked Quadrat Variance Method (Ludwig 1979) and has been chosen by a number of researchers (e.g., Usher and Booth 1986) over other newly developed methods (see Galiano 1982a). Some authors (e.g., Usher 1983), however, wisely caution against wholesale adoption of it. TTLQV is computationally similar to BQV and calculates the variance of cover from r groups of quadrats within $2r$ groups of quadrats. The formula, derived from Ludwig (1979), is

$$\mathrm{Var}(x)_b = (1/(n+1-2b)) \left[\sum_{j=1}^{n+1-2b} 1/2b \left(\sum_{i=j}^{j+b-1} x_i - \sum_{k=j+b}^{j+2b-1} x_k \right)^2 \right]$$

where j is the leftmost position of the left r group of quadrats within

$2r$ groups of quadrats and x_i is the plant density (cover) in the ith quadrat.

Unlike the BQV method, r (block size) is incremented by 1 each iteration rather than by a power of 2. This means that the r and $2r$ blocks overlap along the transect. The BQV method is "wasteful" of data (Hill 1973) (variance is only calculated at block sizes of 2, 4, 8, 16, 32, 64 ...), whereas the TTLQV method calculates the variance at all block sizes. Since tests of significance are not applied, the data can be "re-used" repeatedly (Usher 1983). As with the BQV method, the result is presented graphically as a plot of variance (of cover or density) vs. block size. A peak in the blocked quadrat variance curve indicates a pattern scale approximately at the corresponding block size (see Dale and MacIsaac 1989) while the value of the peak is related to pattern intensity (see below). Galiano (1982a, 1983) and Carpenter and Chaney (1983) mistakenly criticize TTLQV for not detecting patch size.

For a complete presentation of the above methods, consult Ludwig (1979). Other papers by Zahl (1977), Ludwig and Goodall (1978), Cormack (1979), Jupp and Adomeit (1981), Carpenter and Chaney (1983) and Galiano (1983) give comparative reviews of these and other contiguous quadrat methods, while Greig-Smith (1979) examines the concept of "pattern" in ecology.

Dale and MacIsaac (1989) discuss four drawbacks associated with TTLQV, and similar methods, which were substantiated by analysis of artificial patterns. The first three occur in situations of complex pattern (two or more scales).

1. If the smaller scale pattern is not intense, it may be undetected because of the overwhelming larger scale pattern. The peaks associated with the smaller scale pattern may be reduced to shoulders in the curve, or be totally obscured by the larger, more intense pattern. This problem, in which TTLQV emphasizes

larger scale pattern in artificial data, is mentioned by Ludwig (1979) and Carpenter and Chaney (1983).

2. If intensity is considered synonymous with variance, for two scales of similar intensity, the larger scale pattern appears more important (because of larger variances). Patterns of larger scale give larger variance for the same intensity.

3. It has been shown by Usher (1975) and others that there can be a "resonance effect" of smaller scales on larger ones. For a TTLQV peak with variance V at block size b, at block sizes of $3b$, $5b$ and $7b$, the variance contributed by the peak at b is $V/3$, $V/5$ and $V/7$ respectively (Dale and MacIsaac 1989). This may result in detection of false peaks at larger block sizes (Ludwig and Goodall 1978).

4. Relative patch and gap size within the scale is not detectable (Figure 2-7).

New pattern analysis methods presented by Dale and MacIsaac (1989), which complement the TTLQV analysis, overcome all of these concerns.

Older methods equated the pattern intensity at a particular scale with the TTLQV variance at that block size. There are several flaws in this. First, intensity is related not only to the variance, but also to the block size, so that variance by itself does not give intensity. Given two peaks with the same intensity, the variance for each is a function of the square of the block size. Second, if there is more than one scale in a pattern, the intensity at a particular block size is affected by intensity at other block sizes.

A new method (called "peak correction" or "additive decomposition") to determine pattern intensity in relation to scale, is presented by Dale and MacIsaac (1989). This method overcomes Usher's criticisms by

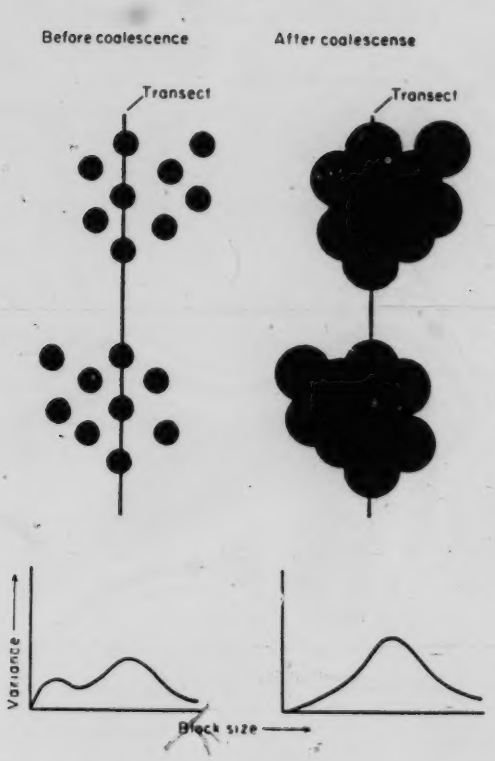


Figure 2-7 Pattern Scale Detection By TTLQV

Two scales of pattern are detected. As the patches coalesce the smaller scale disappears. Gap and patch size is not detected.

Source: Dale and MacIsaac 1989
(Used with permission)

removing the effect of other peaks on the peak in question. For a given peak V at block size b, the intensity can be defined as the difference in density (e.g., % cover) between full and empty quadrats (assuming equal patch and gap size). For example, at block size 16 with an intensity of 4, it means that on average there are 16 empty quadrats and 16 quadrats with 4 % cover in them. If there is a perfect sequence of p dense quadrats and g sparse quadrats, then there is a relationship between intensity (d) and the variance at block size b. The variance at a particular block size is compared to the maximum value one would get with a perfect pattern of equal-sized patch and gap. Given that the perfect pattern for peak V_b is at a block size of $(p+g)/2$, this can be used to estimate d from V_b approximately for imperfect patterns. Based on the assumption that patch and gap are equal, then the estimated intensity associated with that peak is $d = \sqrt{6bV_b/(b^2+2)}$. Even if the patch and gap equality is out by 25%, it only causes a 5% change in d.

In the simplest case, this new method determines the intensity for a given scale (if there is only one scale of pattern) using the above formula. If there are several scales, it can determine the intensity associated for a particular scale by subtracting out intensity contributed by scales at smaller block sizes (since the intensity contributed by several scales of pattern at a given block size is additive). As well, by removing the effects of the first two peaks, this method can determine if a shoulder in the block-variance curve is in fact a submerged peak. This method can be used when the variance-block curve exhibits a plateau with several small peaks. As well, by removing the effect of the two most intense peaks, the resonance effect is removed and only the true peaks remain.

In summary, this "peak correction technique" removes the effect of the two left-most peaks in the variance plot, so that smaller scale, less intense patterns can be detected; it allows more accurate recognition of intensities from several scales of pattern in the same transect; and it removes the effects of spurious peaks caused by

resonance. This peak correction is based on the assumption of additive combinations of the two scales of pattern.

There are some disadvantages to the TTLQV and peak correction technique which have been previously noted for an earlier contiguous quadrat variance method, BQV (Pielou 1977). The first is that pattern analysis at larger block sizes is less precise due to a decrease in degree of freedom. For this reason, all pattern analysis was restricted to block sizes of less than 70 (21 m), which is one quarter of the total transect length. The second is that increases in the centre to centre distance with increasing block size invalidates variance-mean tests. The third is that successive mean squares are not independent, so one cannot test if mean squares from successive block sizes are significantly different. Methods have been proposed by Mead (1974) and Zahl (1974) which would allow for these independent tests of variance.

More recent concerns have also been raised (see Carpenter and Chaney 1983). Most earlier papers state that the block size of the variance peaks is the same as the scale of pattern that gave rise to it. Dale and Blundon (*in press*) have recently shown that in fact the scale of pattern is underestimated by the peak block size, especially at larger block sizes. As they conclude, this should not have any major ecological significance. This may be true in this research, where only the two smallest scales of pattern were examined. Even with the above concerns, these new methods are a major improvement on some earlier techniques.

Detection of patches and gaps requires a second set of techniques. If there is only one scale of pattern, then detection of patch and gap size is simple, using the runs test presented above. For more complicated situations, in which there are patches and gaps corresponding to several scales of pattern, a new method presented by Dale and MacIsaac (1989) is required. A brief synopsis follows.

This method, based on permutations of integers, requires that the

plant cover (densities) of all contiguous quadrats in the transect be presented as a permutation of integers 1,2...*n* (arbitrary ranking of ties does not affect the results). The number of times that a series of integers rises above adjacent integers for a series of length *k* is calculated. For example, the ranking below indicates two 3-ups so that u_3=2.

4,12,8,10,6,1,9,7,13,5,11,3,2

Based on the null hypothesis that all rankings are possible, peaks in a plot of y_k as a function of *k* (which uses the expected value and variance of the *k*-ups) indicate common patch sizes where

$$y_k = [\text{Obs } u_k - \text{Exp } u_k]/\sqrt{\text{Var}(u_k)}$$ (Dale and Moon 1988)

A value greater than 2.0 (based on the 95% confidence level of the normal distribution) indicates consistently re-occurring patches of size *k*. If there are some patches of size *k*, but the pattern is interrupted by areas of bare ground, it may be represented by a "local peak" in the plot of y_k as a function of *k* (less than 2.0, but higher than adjacent values).

In the same way, consistent dips of size *k* in the permutation of integers are used to determine average gap sizes. These methods are used in conjunction with the TTLQV analysis.

There are some perceived minor drawbacks with this method as discussed by Dale and MacIsaac (1989). For example, it is expected that, if the transitions from patch to gap are abrupt then [*p*+*g*]/2=scale. If, however, the boundaries are less well defined, then the [*p*+*g*]/2 > scale, and they propose methods to deal with that.

The pattern analysis results were subjected to standard statistical analysis. Only non-parametric methods were used for the following

reasons: a) It was uncertain if the data met the required assumptions for parametric analysis. b) Most of the output was mathematically manipulated. Two major analyses were done. To test for correlations between pattern attributes and time, Kendall's correlation coefficient was used (Sokal and Rohlf 1981, p.602). This "semi-quantitative" descriptor retains most of the information of the quantitative Pearson's r coefficient (Legendre and Legendre 1983). The Mann-Whitney U test (Sokal and Rohlf 1981, p. 433) was used to test for significant differences in mean values on different-aged surfaces.

2.3 Results

2.3.1 Nucleation

In all nucleation test areas, the G-test rejected the null hypothesis (Table 2-1). In all cases, the distribution of conifer and shrub stems in live *Dryas*, dead *Dryas* and bare ground areas was not in proportion to the relative areas of each cover type ($P < .01$). For all sample sites, the number of stems occurring in dead *Dryas* was much greater than expected, while the number found in bare ground areas was much less than expected. Stem occurrence in live *Dryas* to be slightly greater than expected in four of the six sample sites. This trend is also shown in the overall average (Table 2-1).

2.3.2 Pattern Development[3]

The runs test results were consistent for all species groups at the Southeast Lyell and Icefield sites. In all cases, the number of runs was significantly less than expected ($P < .05$), which means that the *Dryas drummondii* and all the species groups showed some degree of segregation into patches and gaps, and could then be examined using the pattern

[3]Pattern components related to the smallest and second-smallest scale of pattern will be designated as "1" and "2", respectively.

TABLE 2-1

SOUTHEAST LYELL NUCLEATION TESTING

G TEST (Log - Likelihood Ratio Test)

Ho: Number of stems in each cover type proportional to cover.
H1: Number of stems in each cover type not proportional to cover.

		Cover Type				
		Live Dryas	Dead Dryas	Unvegetated	Total	Test Statistic [4]
Area 1	% Cover [1]	49.2	14.8	35.8	99.8	
	Observed No. of Stems [2]	49	26	26	101	G (adj) = 9.80*
	Expected No. of Stems [3]	49.8	15.0	36.2	101	
Area 2	% Cover	59.5	7.6	32.4	99.6	
	Observed No. of Stems	69	32	9	110	G (adj) = 67.80*
	Expected No. of Stems	65.5	8.4	35.7	110	
Area 3	% Cover	46.1	7.8	46.1	100.0	
	Observed No. of Stems	37	31	5	73	G (adj) = 91.97*
	Expected No. of Stems	33.7	5.7	33.6	73	
Area 4	% Cover	47.3	6.1	46.0	99.3	
	Observed No. of Stems	23	13	4	40	G (adj) = 39.77*
	Expected No. of Stems	18.9	2.4	18.4	40	
Area 5	% Cover	41.4	4.9	53.7	99.9	
	Observed No. of Stems	140	42	92	274	G (adj) = 68.95*
	Expected No. of Stems	113.3	13.3	147.2	274	
Area 6	% Cover	78.1	7.4	13.9	99.4	
	Observed No. of Stems	67	38	12	117	G (adj) = 63.09*
	Expected No. of Stems	91.4	8.7	16.2	117	

1 % cover each type
2 Number of stems growing in each cover type
3 Expected number of stems (based on proportion of each cover type)
4 G is reduced by Williams Correction
Critical value (two-tailed test) X^2 .01, 2 = 9.21

analysis methods.

2.3.2.1 Columbia Icefield Site

The development of *Dryas* pattern for the Sunwapta and Dome chronoseqences at the Columbia Icefield followed similar trends (Tables 2-2 and 2-3), although there are some discrepancies. Scales of pattern (both 1 and 2) at both locations were quite consistent on surfaces younger than 60 years. On older surfaces, they decreased slightly (especially the smaller scale). In almost all cases, the smallest scale was detected by quadrat variance analysis only after the variance due to the two larger scales was removed.

Pattern intensity was more variable; at the Sunwapta site, the maximum intensity (both 1 and 2) occurred on the Terrace B where total *Dryas* cover is near 50%. This trend was not present in the grouped results for the Dome site (Table 2-3).

At both sites, patch 1 and 2 generally increased until approximately 50 years (*Dryas* cover 75%), followed by a slight decline on older surfaces (even though total cover was maintained). The only significant maximum was at the Dome site for patch size 1 ($P < 0.5$). As expected, the gap results were a mirror image of the patch. Most of the patches and gaps were detected only by 'local' peaks in the analysis.

Pattern complexity (as identified by the average number of detected scales of pattern) was slightly lower on the intermediate-aged surfaces at both sites (Tables 2-2 and 2-3). This trend was also apparent when only the initial TTLQV peaks were considered.

Table 2-4 provides a more detailed analysis of the smallest scale of pattern on intermediate-aged surfaces at both the Icefield sites. At the Dome site, the scale, intensity and patch size were consistent among the

TABLE 2-2

PATTERN COMPONENT AVERAGES FOR THE SUNWAPTA RIVER SITE

(*Dryas drummondii*, Two Smallest-Scale Patterns) [1]

Terrace	A	B	C	D
Number of Transects	3	4	2	1
Age	18	31	43	117
Total Dryas Crown Cover (%)	3.0	45.9	74.9	78.5
Scale 1	2.1	1.9	2.0	1.2
Intensity 1	13.0	50.7	38.9	37.4
Patch 1 Size	2.1	1.9	3.2	0.9
Gap 1 Size	2.8	2.0	1.2	1.8
Scale 2	6.6	7.6	6.0	4.2
Intensity 2	6.4	38.8	28.3	30.7
Patch 2 Size	3.3	7.4	8.4	5.7
Gap 2 Size	10.4	8.8	3.8	2.7
Number of Scales	4	3	4	4

1 Scale, patch and gap are in metres.
Analysis based on total live plus dead crown cover.

TABLE 2-3

PATTERN COMPONENT AVERAGES FOR THE DOME GLACIER SITE

(Dryas drummondii, Two Smallest-Scale Patterns) [1]

Surface	Young Age Surface	Intermediate Age Surface	Old Age Surface
Number of Transects	4.0	3.0	3.0
Age	37.3	55.6	94.0
Total Dryas Crown Cover (%)	26.7	80.3	88.8
Scale 1	1.8	2.3	1.4
Intensity 1	32.9	29.8	29.0
Patch 1 Size	2.0	3.7	2.3
Gap 1 Size	2.6	1.4	0.9
Scale 2	5.4	5.7	5.5
Intensity 2	25.6	20.1	24.1
Patch 2 Size	4.8	7.2	5.6
Gap 2 Size	6.4	4.8	2.4
Number of Scales	4	3	4

1 Scale, patch and gap are in metres.
Analysis based on total live plus dead crown cover

TABLE 2-4

PATTERN INTENSITY AND PATCH-GAP ANALYSIS

OF DRYAS DRUMMONDII AT THE COLUMBIA ICEFIELD

(Intermediate-Aged Surfaces, Smallest-Scale Pattern) [1]

a) Sunwapta River Terrace Site - Terrace B

Transect	Age	% Dryas Cover	Scale 1	Patch 1 Size	Gap 1 Size	Intensity 1
B-1	27	15.3	2.1	(1.8)	2.4	56.0
B-2	30	53.8	1.8	(2.4)	(1.5)	51.8
B-3	30	42.8	1.8	1.2	2.4	62.7
B-4	35	71.5	1.8	(2.1)	(1.8)	31.8

b) Dome Glacier Outwash Site - Middle Aged Surfaces

Transect	Age	% Dryas Cover	Scale 1	Patch 1 Size	Gap 1 Size	Intensity 1
Dome - 5	52	75.5	2.7	(3.9)	(2.1)	33.2
Dome - 6	55	85.4	2.4	(3.9)	(0.9)	25.7
Dome - 7	60	79.9	1.8	3.3	(1.2)	30.4

[1] Brackets indicate local peaks.
Scale, patch and gap are in metres.
Analysis based on total live plus dead crown cover.

three transects. At the Sunwapta site, the *Dryas* cover ranged from 15% to 71%, even though the ages were within an eight year range. This was reflected by differences in the pattern components along each transect. Total *Dryas drummondii* pattern analysis results for the Dome and Sunwapta chronosequences (two smallest scale patterns for individual transects) are in Appendix 2-2 and 2-3, respectively.

2.3.2.1 Southeast Lyell Site

At the Southeast Lyell site up until year 70, the *Dryas* development was similar to that at the Icefield (Table 2-5): 1) Intensity 1 and 2 reached maximum at year 25 when cover nears 50%. 2) Patch size generally increased and gap size declined over time. Unlike the Icefield sites, *Dryas* reached near 100% cover at year 40, then declined to less than 1% cover on the 143-year-old terminal moraine. This was reflected in the pattern results for the older surfaces. Unlike the Icefield sites, scale (especially the larger one) was not constant: both scales 1 and 2 peaked at year 90 during the phase of *Dryas* decline. As well, intensity 1 and 2 had a bimodal trend, with peaks around 25 and 100 years. Pattern scale values were all within the same range, however, along the three chronosequences (scale 1: 1.2-3.2 m, scale 2: 4-8 m).

For the non-vascular species group, intensity increased almost constantly (Table 2-6). Scale and patch size declined on intermediate-aged surfaces before reaching a maximum on the oldest surfaces. With the shrub group (excluding *Dryas drummondii*), both scale and intensity increased until 110-140 years when cover peaked at 55% (Table 2-7). Conifer results were similar (Table 2-8), except that the maximum values for scale 1 and 2 occurred slightly earlier and intensity 2 did not reach a maximum until the old-growth forest.

There are general trends present among several species groups at the Southeast Lyell site which should be noted. The smallest scale tended

TABLE 2-5

DRYAS DRUMMONDII PATTERN SUMMARY
FOR THE SOUTHEAST LYELL GLACIER SITE
(Two Smallest-Scale Patterns)[1]

Transect	Age	Total Cover (%)	Scale 1	Scale 2	Intensity 1	Intensity 2	Patch 1	Patch 2	Gap 1	Gap 2
1a,b	6	0.3	1.8	8.1	0.4	0.3	2.1	--	1.5	--
2a,b	23	41	2.3	8.1	38.8	51.1	1.4	7.8	3.5	8.4
3a,b	38	96	1.8	3.9	13.3	9.4	2.1	4.8	1.7	3.2
4a,b	43	97	1.2	4.5	13.5	6.0	1.2	6.8	1.2	2.2
5a,b	47	93	1.7	4.4	15.7	9.7	2.7	6.2	0.8	3.0
6a,b	53	93	3.2	7.8	18.2	10.3	6.2	11.8	1.1	3.8
7a,b	66	92	1.2	4.5	22.0	15.7	1.2	7.5	1.2	1.8
8a,b	80	85	1.2	6.3	29.3	26.7	1.5	8.6	1.2	4.0
9a,b	89	76	5.3	12.2	34.0	26.5	8.3	--	2.9	--
9c	109	30	1.8	4.2	30.1	45.8	2.7	3.9	1.5	4.5
10a,b	129	20	2.4	6.2	21.0	35.9	2.1	2.4	2.7	10.4
11a,b	143	0.8	2.7	8.3	6.9	5.7	--	--	--	--
12a,b	432+	0	--	--	--	--	--	--	--	--

1 Analysis based on total live plus dead crown cover.
Results for scale, patch and gap are in metres.
-- Pattern not detected.

TABLE 2-6

NON-VASCULAR PLANT PATTERN SUMMARY
FOR THE SOUTHEAST LYELL GLACIER SITE
(Two Smallest-Scale Patterns)[1]

Transect	Age	Total Cover (%)	Scale 1	Scale 2	Intensity 1	Intensity 2	Patch 1	Patch 2	Gap 1	Gap 2
1a,b	6	0	--	--	--	--	--	--	--	--
2a,b	23	0.7	4.2	13.8	1.5	1.4	1.6	--	6.8	--
3a,b	38	1.7	2.9	5.1	5.5	4.0	1.8	2.4	4.0	7.8
4a,b	43	1.8	0.9	3.5	6.9	4.4	--	1.5	--	5.9
5a,b	47	3.7	2.0	3.6	7.9	4.5	0.8	1.5	3.3	5.9
6a,b	53	3.4	1.4	5.1	10.0	4.8	1.1	3.2	2.0	7.4
7a,b	66	2.9	1.7	5.3	6.6	4.8	0.9	3.4	2.7	7.2
8a,b	80	4.7	1.8	5.1	10.0	6.9	1.2	3.2	2.4	7.1
9a,b	89	4.8	1.8	5.3	11.7	7.3	1.7	3.0	2.0	5.6
9c	109	28	3.6	17.7	26.9	33.9	1.5	--	6.3	--
10a,b	129	26	4.5	13.8	21.7	18.7	1.8	--	7.5	--
11a,b	143	31	2.0	5.7	31.0	24.9	1.5	3.6	2.6	7.5
12a,b	432+	67	3.3	9.0	22.6	49.8	3.7	9.0	2.9	9.9

1 Based on cover of all bryophyte plus lichen species.
Results for scale, patch and gap are in metres.
-- Pattern not detected.

TABLE 2-7

SHRUB PLANT PATTERN SUMMARY
FOR THE SOUTHEAST LYELL GLACIER SITE
(Two Smallest-Scale Patterns)[1]

Transect	Age	Total Cover (%)	Scale 1	Scale 2	Intensity 1	Intensity 2	Patch 1	Patch 2	Gap 1	Gap 2
1a,b	6	0	--	--	--	--	--	--	--	--
2a,b	23	0.01	--	--	--	--	--	--	--	--
3a,b	38	0.5	2.7	5.4	4.5	2.3	--	--	--	--
4a,b	43	1.4	1.4	3.8	11.1	7.7	--	--	--	--
5a,b	47	1.8	1.8	5.4	14.0	8.3	--	--	--	--
6a,b	53	3.8	2.9	8.3	21.2	15.4	2.5	7.9	3.3	8.7
7a,b	66	3.8	2.3	6.5	17.9	20.3	--	1.6	--	11.4
8a,b	80	6.8	1.5	4.4	30.1	12.3	--	2.0	--	6.8
9a,b	89	11	1.8	3.3	37.7	19.1	1.5	2.6	2.1	4.0
9c	109	32	1.2	3.0	41.0	61.5	--	3.3	--	2.7
10a,b	129	55	2.9	11.4	50.8	42.1	3.0	--	3.0	--
11a,b	143	36	3.9	18.6	40.3	41.7	2.0	--	5.8	--
12a,b	432+	40	3.3	11.3	41.9	47.9	2.9	--	3.7	--

1 Based on species of shrub growth form (all heights), excluding *Dryas drummondii*.
Results for scale, patch and gap are in metres.
-- Pattern not detected.

TABLE 2-8

CONIFER PLANT PATTERN SUMMARY
FOR THE SOUTHEAST LYELL GLACIER SITE
(Two Smallest-Scale Patterns)[1]

Transect	Age	Total Cover (%)	Scale 1	Scale 2	Intensity 1	Intensity 2	Patch 1	Patch 2	Gap 1	Gap 2
1a,b	6	0	--	--	--	--	--	--	--	--
2a,b	23	0.8	1.2	5.1	2.9	1.1	--	--	--	--
3a,b	38	4.8	1.5	3.3	16.1	9.5	--	--	--	--
4a,b	43	8.7	1.2	3.9	32.9	17.8	1.0	2.5	1.4	5.3
5a,b	47	8.2	1.4	3.6	32.3	28.5	--	1.5	--	5.7
6a,b	53	12	1.8	3.9	43.8	23.8	1.0	2.1	2.6	5.9
7a,b	66	20	2.0	5.0	45.7	42.6	0.9	--	3.1	--
8a,b	80	24	1.4	4.2	48.9	44.4	--	2.3	--	6.8
9a,b	89	38	3.0	9.2	50.6	54.9	2.1	--	4.5	--
9c	109	46	2.4	8.1	60.4	41.3	3.3	--	1.5	--
10a,b	129	43	2.4	6.6	44.7	53.0	2.7	2.0	2.3	1.8
11a,b	143	63	1.8	3.6	57.0	43.7	2.0	4.8	2.0	2.4
12a,b	432+	60	1.4	3.6	38.4	67.0	1.6	3.3	1.2	3.9

1 Based on all coniferous species of tree growth form (all heights). Results for scale, patch and gap are in metres.
-- Pattern not detected.

to be more consistent (less variable) than the larger scale. For all groups, scale 2 was initially large, declined on the intermediate-aged surfaces and then increased to a higher maximum on the older surfaces. This was also true for scale 1 for *Dryas* and non-vascular groups. Except for *Dryas*, the two scales had a maximum at the same time; unlike the Icefield sites, they were not constant over time.

Trends in pattern were the least variable of the pattern descriptors. In all four species groups, maximum intensity 1 occurred when the cover was relatively close to 50% and it always peaked before intensity 2 (Tables 2-5 to 2-8). The non-vascular, shrub and conifer species groups all had a significant positive correlation ($P < 0.01$) between surface age and intensity 1, intensity 2 and total cover. Maximum intensity always occurred after 90 years; in some cases, however, it decreased on the oldest surfaces. Conifers had the most intense pattern and *Dryas* and non-vasculars the least.

Based on the runs test, it was known that along all transects, the plant cover for each species group was segregated into patches and gaps. The patch and gap sizes were not well detected, however, by the Dale and MacIsaac's (1989) method, especially for the shrub and conifer groups. Patch and gap sizes were best recovered on the intermediate-aged surfaces when cover of the species group was around 50%. In any case, most of the values were from local peaks in the analysis. Patch-gap analysis for *Dryas* reflected the trend in abundance: largest patches on the intermediate-aged surfaces, largest gaps on the young and old surfaces. The other three groups all had a tendency for larger patches and smaller gaps with older age surfaces, although there were no significant trends ($P > 0.01$).

The total number of scales was highest for the species groups on the following surface ages: conifer- 40 years, *Dryas drummondii*- 50 years, non-vasculars- 80 years, shrubs- 90 years. In all cases the peak number of scales occurred at the same time for both the initial TTLQV peaks and

after the peak correction technique was applied. Some initial TTLQV variance-block size graphs had high numbers of peaks (>10), especially on intermediate-aged surfaces. This may be due to resonance (Usher 1975), or several peaks close together may only represent one pattern scale in reality. In any case, they are not ecologically meaningful (M. Dale, pers. comm.). Therefore, when several peaks occurred very close together, only the most intense one was chosen for inclusion in the results. Also included in the results were the small-scale patterns which only appeared as "shoulders" in the original TTLQV curves, but which can have ecological importance (Usher 1975). Southeast Lyell pattern results for the four species groups (arranged into five surface ages) are presented in Appendix 2-1.

Picea engelmannii and *Abies lasiocarpa* cover under 5 m tall on different surfaces was not significantly different ($P > 0.5$) between different-aged surfaces. As well, these two parameters did not have a significant correlation ($P > 0.01$) with surface age.

2.4 Discussion

Since the runs test indicated patchiness for all four species groups, for all transects on all sites, this seems to support Greig-Smith's (1979) assertion that pattern is universal. This is also born out by the TTLQV analysis, which indicated that almost all transects had at least one scale of pattern (indicated by presence of peaks in variance-block graphs). This is supported by many other papers published on vegetation pattern research (e.g., Galiano 1986), which conclude that clumping is common. Although this may be considered self-evident by some researchers, it should be initially tested before pattern analysis is done.

This research may represent one of only a few studies which test all the components of pattern (scale, intensity and patch/gap) using methods

based on contiguous quadrats. Many studies have used just one method to study pattern (e.g., Greig-Smith's blocked quadrat variance method). This research used four: 1) runs test: determines significant patchiness, 2) TTLQV: detects pattern scale, 3) peak correction technique: to clarify pattern scale and 4) patch/gap analysis. Other methods such as those to quantify pattern irregularity (Dale and Blundon *in press*) are being developed. This approach using multiple methods is recommended by many authors (e.g., Usher 1975, Ludwig and Goodall 1978). As suggested by Usher (1983), this approach is best used with simple communities of one or two species, to test pattern development theories (e.g., Greig-Smith's model).

Austin (1981) makes a strong case that the best way to study the spatial component of vegetation dynamics is by permanent quadrats. While the general history of vegetation development is known for the study sites (see Section 1.3.4 and 1.3.6) a detailed quantitative record was not available. Therefore, if a change in pattern was observed on two different-aged surfaces (sampled at the same time), it could not be inferred, with certainty, that the pattern on the older surface was once the same as the pattern on younger surface. This limitation was unavoidable, given the time constraints on the research. It may be concluded, however, that if the environmental conditions were kept relatively constant, the older surface pattern had developed from pattern which was once <u>similar</u> to that observed on the younger surface.

2.4.1 Nucleation Hypothesis

Conifer and shrub species density (stems/m^2) is significantly greater in *Dryas drummondii*[4] areas than in bare ground areas for all six sample locations at the Southeast Lyell site (Table 2-1). Although not tested statistically, field evidence indicates that this situation also occurs at the Columbia Icefield site. For example, a tally of 20 *Picea*

[4] For simplicity, if one species in a certain genus is being discussed, then only the generic name will be used.

seedlings along transect Dome-10 showed them all growing in dead *Dryas* areas (dead *Dryas* cover is 46% on that transect). In spite of this positive association between *Dryas* clones and conifer and shrub species, there is no statistical evidence to support *Dryas* facilitation in the establishment of woody species. This could not be tested without using permanent plots with individually tagged plants. Without this, even if a shrub is growing in dead *Dryas*, there is no way to ascertain accurately which species established first. To compound this, comparative root ages of *Dryas*-conifer pairs could not be done because the root crowns of *Dryas* clones usually start to decay after 35 years (Wilson 1978). As well, when conifers are found in the dead centres of *Dryas* clones, it may be that the conifer sapling is the cause of the *Dryas* senescence, due to shading and needle shedding.

A second approach is to compare association from *Dryas*-centred plots with those of random plots (Blundon 1989). This method can detect asymmetric association (e.g., *Picea*-dependent *Dryas* vs *Dryas*-dependent *Picea*) and is an intermediate approach between the random quadrat method used in this research and the permanent plot method recommended above.

In spite of the lack of experimental evidence, there is some qualitative support in the literature for nucleation. N-fixing species such as *Hedysarum mackenzii*, *Dryas drummondii* and *D. octopetala* are purported to act as "centres of recruitment" for other species (Sondheim and Standish 1983). Qualitative descriptions of the nucleation effect by *D. drummondii* on deglaciated terrain have been noted for other sites (Cooper 1939 cf. Austin 1981, Lawrence 1958 and Heusser 1956). As Austin (1981) states, this process may not be restricted to the "facilitation" mechanism as proposed by Connell and Slatyer (1977). It may be part of a hierarchy of causes as described by Pickett et al. (1987).

The effect of *Dryas* on site stability and soil development (including organic matter and nitrogen accumulation, trapping of fine material, and moisture retention) is well documented (e.g., Anderson

1967b, Wilson 1978, Watson et al. 1980). There is evidence that a well-developed *Dryas* mat creates seedbed conditions favourable to establishment of *Abies lasiocarpa* and *Picea engelmannii*. Seedling mortality of these conifer species is greatly increased by needle-ice, frost heave and soil moisture deficits (Patten 1963, USFS 1965, Nobel and Alexander 1977), whereas germination is greatly enhanced on moisture-retentive seedbeds (Day 1964). Since both species can establish on duff substrates (USFS 1965), such as decaying *Dryas* mats, it seems logical that *Dryas* would help in this establishment.

Dryas appears to act as a centre of recruitment for other woody species such as *Shepherdia canadensis*. It may also facilitate the establishment of some non-vascular species. At both study sites, acrocarpous mosses such as *Ceratodon purpureus* are first noticeable in the decaying centres of *Dryas drummondii* clones. They are later replaced by pleurocarpous mosses (e.g., *Drepanocladus uncinatus*).

Notwithstanding the above, the nucleation role of *Dryas drummondii* and its effect on pattern at the study sites is probably not as important as first thought due to two reasons: 1) Except in severe climatic conditions (e.g., Icefield site), the *Dryas* stage is soon replaced by later seral stages. 2) Subsequent stages will occur even without *Dryas*. These factors are discussed in turn.

Most of the published examples of nucleation involve longer-lived species (often clonal) which, over a period of time, modify the micro-environment sufficiently for other species to establish. Unlike those of *Dryas drummondii*, these clonal patches are relatively self-sustaining. (*Dryas* is not self-sustaining, perhaps, because it has only one tap root, with weakly developed adventitious roots. This tap root is where the decay usually begins.) These longer-lived species include *Juniperus virginiana* on old stabilized sand dunes (Yarranton and Morrison 1974), rain forest species invading savanna vegetation (Kellman 1978 cf. Miller 1978) and *Pteridium aquilinum* and *Calluna vulgaris* in heathlands (Watt

1947b). The latter example is a cyclical phenomenon in which the former species periodically undergoes a rebuilding phase. The most widespread example of nucleation is vegetation stripes in arid regions (Austin 1981) composed of trees or shrubs, interspersed with bare areas.

Although the decay in the older *Dryas* centres is characteristic of many clonal species (Bell 1984) its relatively short life span is not (Silvertown 1982). In the 80 years in which it dominates, it probably does not affect the substrate sufficiently to entrain the pattern of subsequent vegetation. Yarranton and Morrison (1974) developed their initial concept on a successional sequence which required almost 3000 years for development of the climax forest. The nucleation study here is several orders of magnitude shorter, and so may not be comparable. Yarranton (pers. comm.) cautions against looking for complex answers for simple phenomena.

There is a distinction to be made between qualitative and quantitative nucleation and facilitation. In the qualitative context, the following question is addressed: "Is a particular species required for establishment of the subsequent species?" This is a yes-or-no situation. In the quantitative context, it is asked "How much does the particular species enhance or accelerate growth of subsequent species?" Quantitative facilitation can be termed "enhancement" or "non-obligate" (Blundon 1989). This is concerned with the effect of one species on the rate of development of the second. In this latter case, rate functions, magnitudes and amounts could be assigned to the facilitation or nucleation process (hence the term "quantitative").

In most published examples of nucleation in other environments, it appears that the qualitative facilitation mechanism (Connell and Slatyer 1977) is operative (i.e., not all species are able to establish on the early post-disturbance environments). In this research at the Southeast Lyell Glacier, however, all the main species in the successional sequence (except non-vasculars) appeared on recently deglaciated

surfaces. In addition, conifers became established on young surfaces even without *Dryas*. In this case, nucleation did not appear to occur. In southeast Alaskan sites, although *Dryas* is initially widespread, later successional stages such as alder thicket or spruce-hemlock communities will develop even with *Dryas* absent (Crocker and Dickson 1957). While the amount of N contributed to the soil at the alder thicket stage at Glacier Bay may be substantial (62 kg/ha/year) (Crocker and Major 1955), it is not essential for forest development. Qualitative facilitation does not appear to operate at with *Dryas* at these study sites.

In terms of qualitative nucleation and facilitation, the answer is less obvious. Lawrence et al. (1967) suggest that in southeast Alaska, *Dryas* accelerates the rate of succession to fully developed forest by 20-30 years. Facilitation at the Mount Robson Moraines is probably qualitative (Blundon 1989). This may be similar at the Southeast Lyell sites, but since *Dryas* was almost ubiquitous, this hypothesis could not be investigated.

Unlike the situation at Glacier Bay (Crocker and Major 1955) there were no major signs of nutrient deficiency with early colonizers (e.g., *Picea* seedlings) at any of the study sites. Also, coniferous saplings growing in *Dryas* clones did not appear more lush. The more chlorotic saplings were always in open, exposed microsites, so that environmental factors such as wind desiccation appeared to be the major stresses. Tisdale et al. (1966) support this by reporting that the difference in growth of trees and shrub are mostly due to the effects of wind and snow. Field evidence such as flagging and asymmetric desiccation damage support this idea. During reconnaissance to the study sites in February 1985, evidence of winter desiccation and snow abrasion damage similar to that reported by Sakai (1970) (e.g., brown stems and needles) was noted on conifer saplings in exposed areas.

In these post-glacial environments, small-magnitude mass movement processes continue to act on the surface long after glacial recession

(Welch 1967). As well, other destabilizing processes such as needle-ice formation can hinder vegetation establishment (Sigafoos 1952, Brink et al. 1967). Along with the above, there is ample evidence of the effect of strong winds, especially at the Icefield site. This includes strongly flagged saplings, desiccation damage (especially in winter), flipped over *Dryas* clones and surface deflation (resulting in "stony pavement" (lag gravels) as noted by Crocker and Major 1955). In such an environment, surface stability is probably a major factor in vegetation establishment. If *Dryas* helps stabilize the soil surface (section 1.3.6), then it probably accelerates the enhancement of other species.

In light of the above, micro-site stability may be another reason why *Dryas* had positive association with other woody species; both *Dryas* and conifers co-occur in what could be described as more stable micro-sites. At both study sites, conifers and shrub species appear to be most successfully established on coarser-textured surfaces, especially adjacent to larger rocks (Plate 2-1). Generally, *Picea* saplings are establishing where *Dryas* is, although they may not be facilitated by *Dryas*. The role of soil (or surface) heterogeneity on species establishment and development cannot be overstated (Harper 1977).

Dryas does alter micro-conditions somewhat, to provide better sites for conifers (facilitation), but both species are more probably just co-occurring in suitable microsites (tolerance). This latter suggestion is an alternative hypothesis, in which all the species are exhibiting a similar ecological amplitude. Because of the environment, the physical stabilization role of *Dryas* is probably more important than the nutrient role. More study is needed before conclusions can be drawn about why the conifers appear in the *Dryas* centres. In one way it could be considered inhibition (Connell and Slatyer 1977), in which the conifers can only germinate when the *Dryas* is declining. This is unlikely, given the early establishment of conifers at the Southeast Lyell site. An alternative approach, is that *Picea* inhibits the *Dryas* (through shading), after the *Dryas* facilitates the *Picea*.

At the Sunwapta River site, numerous saplings of *Picea engelmannii*, *Salix glauca* var. *villosa*, and *Shepherdia canadensis* were well established in the 30 year-old cobble berm along the southwest shoulder of the Icefield Parkway highway (Plate 1-4). As well, these berm areas often had high cover of live *Dryas*. On adjacent outwash surfaces, which were usually older and finer-textured, the *Dryas* cover was discontinuous and the shrub and conifer density was much lower. This difference in development appears to be related to better stability and shelter from the wind, for the following reasons. The uneven stony berm surface may produce a thicker boundary air layer than on the more exposed outwash surfaces. This would provide a more sheltered micro-sites for shrub establishment in this windy environment. Saplings in this location were not flagged under 1 m height, which supports this argument. In terms of stability, needle-ice was not observed on the cobbley surface. Soil moisture differences also do not appear to be a factor. Snow pack depth, measured in February 1985, was not any greater along this berm than on adjacent surfaces. As well, mesic areas along the outwash did not have noticeably greater shrub and conifer density. For these reasons, conifer and shrub establishment along the berm does not appear to be related to favourable moisture conditions.

In this windy environment, conifers require a stable site for successful development. This phenomena can be described as "physical facilitation", as opposed to "biological facilitation" (G. La Roi, pers. comm.). Other researchers (e.g., Sprague and Lawrence 1959, Worsley and Ward 1974) note that on recently deglaciated environments, shrubs such as *Alnus sitchensis* and herbaceous plants are usually found beside larger cobbles and boulders. At the Southeast Lyell site, conifers and shrubs of all sizes from all surface ages were often established by large cobbles and stones. It is, however, difficult to separate the relative effects of exposure, moisture, aspect and their effects on species distribution and pattern.

Plate 2-1 *Picea engelmannii* (117 years old) by Boulder on Terrace D, Sunwapta River Site. August 1984

Plate 2-2 *Dryas* Establishment Along Channel Riser, Sunwapta River Site. August 1984

Nucleation, as described by Kirby (1977) in which a forest front advances onto an old field, appears to be occurring along the northeastern edge of Terrace D. In a 10 m band along the outwash surface adjacent to the forest margin, there is a higher density of plants including *Picea*, *Arctostaphylos* spp. and other shrubs. Over time, this may expand the forest margin right to the highway.

At both the Icefield and Southeast Lyell sites, all the major shrub and conifer species had their earliest and best development along the edge of the abandoned meltwater channels or along the base of moraines. This may relate to the stability theory, but these plants may also be establishing in locations where seeds would be lodged after transport by water.

2.4.2 Pattern Development

2.4.2.1 Columbia Icefield Site

Similar pattern development trends at both the Icefield sites, were detected by the pattern analysis methods. Pattern development at the Dome site is, however, less clear (i.e., more variable) than at the Sunwapta site (compare Tables 2-2 with 2-3 and 2-4 part a with 2-4 part b). This may be due to the less well-defined age gradient (see Section 1.3.4) and greater environmental heterogeneity at the Dome site. Although *Dryas* cover does increase from young to old surfaces ($P < .01$) the sequence of development and associated cover is confounded by variations in surface materials, exposure and moisture conditions. Vegetation development is a function of surface age as well as clast size, microtopography, soil moisture, exposure and surface stability. The largest, most circular *Dryas* clones are on surfaces of intermediate texture; the highest cover, however, is in cobble areas. It is not known if this is reflected in differences in root development.

Pattern development of *Dryas drummondii* at both the Icefield sites is consistent with Greig-Smith's model of the initial stages of pattern development. The initial increase in pattern intensity and patch size and the consistency in scale all accord with this model. There are some marked differences, however: (1) *Dryas* never reaches 100% cover; this explains why the smallest scale does not disappear as predicted by Greig-Smith. (2) Due to cyclical regeneration, the *Dryas* cover stabilizes around 80% on the older surfaces rather than declining as shown in the model. This is why a second increase in intensity does not occur. Another confounding factor is that *Dryas* development does not appear to be uni-directional. There may be episodic dieback associated with periods of more severe climate or pathogens. This may explain the large areas of dead *Dryas* on some of the Dome Glacier transects. The large dead patches may just be, however, normal mortality for clones of a finite lifespan.

Throughout the two chronosequences, patch and gap size is not strongly expressed. They are usually represented only by "local peaks" in the analysis for each transect as defined in section 2.2.4 (i.e., values of y_k). As Dale and MacIsaac (1989) observed, this is probably a function of interrupted and irregular pattern caused by topographical variation and variability in patch and gap sizes because of ongoing recruitment. *Dryas* exhibits interrupted pattern with aggregations along channel risers, separated by areas of sparser cover along channel bottoms and gravel bars (Plate 2-2). Further refinements to account for the effect of pattern irregularity on patch size are being developed (Dale and Blundon *in press*). The decrease in scale on the older surfaces is probably due to the senescence and breakup of older, larger *Dryas* mats (e.g., along the oldest Dome transect, dead *Dryas* cover is 46%) (Appendix 2-3).

The lower pattern complexity on intermediate-aged surfaces at both Icefield sites may be related to maximum growth and coalescence by *Dryas* clones. Both the younger and older surfaces may have a wider variety of

patch and gap sizes due to variable establishment dates in the former and variable recolonization dates in the latter.

The effect of environmental heterogeneity on pattern development of *Dryas drummondii* at the Icefield sites is strong. It appears that physical habitat controls plant cover, larger pattern scale and patch and gap sizes. Initial *Dryas* establishment is almost always along the base of the sides of abandoned river channels (Plate 2-2). By clonal expansion and subsequent infilling, it may eventually cover the entire surface. The orientation, width and spacing of these old channels is, however, undoubtedly the major control on the larger scale pattern. Game et al. (1982) describe a similar process of colonization on abandoned surface mine spoils, where *Dryas* patches join first in elongated strands in sheltered ravines before expanding and coalescing on the upper surfaces. This type of expansion is also seen with *Dryas drummondii* on old highway cutbanks in the study region.

Even at the scale of morphological pattern (1-3 m), surface texture has a strong effect on clonal growth form. Compactly branched, radially symmetrical clones on finer gravels (Plate 2-3) contrast with irregular string forms among boulders and cobbles (Plate 2-4). The latter is an example of "coarse-grained" sample strategy (Harper 1977, p. 238). The fact that plants respond morphologically to these environmental variations is well established (Schlichting 1986). The variation in environmental conditions may affect patch size (i.e., pattern of growth), but not total plant cover (Galiano 1983, 1986). A species may exhibit different strategies of spatial occupation depending on environmental conditions (Smith and Palmer 1976). Plastic variations in shoot module architecture of *Dryas drummondii* have been noted by Crack (1977) in similar habitats and are generally labelled as "phalanx" vs. "guerrilla" growth forms by Lovett Doust (1981), for obvious reasons. This situation may influence the results of pattern analysis. For example, in transects dominated by guerrilla growth forms, the patches are much more diffuse and may not be detected by the patch analysis

while the pattern intensity would be reduced. This may be reflected by the lack of well defined patches at the Icefield. As well, clonal decay in coarse textured areas is more diffuse and does not always originate in the central portions. Often areas similar in age can have quite different cover (Appendices 2-2 and 2-3).

The process of *Dryas drummondii* decline is not a reverse of the growth process. In most cases, except in areas of large cobbles or stones, the *Dryas* clones expand radially. However, the senescence is much more patchy. Although they usually start to die off in the centre, patches of lateral growth often decay at once, resulting in a mosaic of dead and live areas within the clone. It was for this reason (to avoid obscuring pattern trends) that *Dryas* pattern was analyzed using total cover. Even with this approach, the pattern on older surfaces in which there is more dead *Dryas* was less well defined than on younger surfaces. (Pattern analysis was also done using live *Dryas* shoot cover only. The results were similar to those using live plus dead cover, but, for the reasons above, the trends were less well defined.)

Examples of cyclical succession, similar to that found at the Icefield have been reported for other areas of severe climate (e.g., Anderson (1967a): *Dryas drummondii* in Iceland, Usher (1983): moss-turf communities in Antarctica, Viereck (1970): shrub tundra communities in Alaska). The succession is modulated due to strong winds (*Dryas* flip), desiccation and needle-ice. In alpine environments, *D. octopetala* is susceptible to deflation through needle-ice formation (Kuchar 1975). This is because it does not from a continuous litter layer, as do heaths. It results in a discontinuous cover in which the *Dryas* is constantly re-colonizing the bare areas (Kuchar 1975). This is the mechanism operating at the Icefield sites.

Although *Dryas drummondii* is very drought-resistant and is well adapted to these environments (Wilson 1978), it does appear to favour more mesic sites. At both the Icefield sites (especially Dome), *Dryas*

Plate 2-3 Large *Dryas drummondii* Clone, Sunwapta River Site. Clone is approximately 3 m in diameter. August 1984

Plate 2-4 *Dryas drummondii* Clone on Cobble Surface, Dome Glacier Site. August 1984

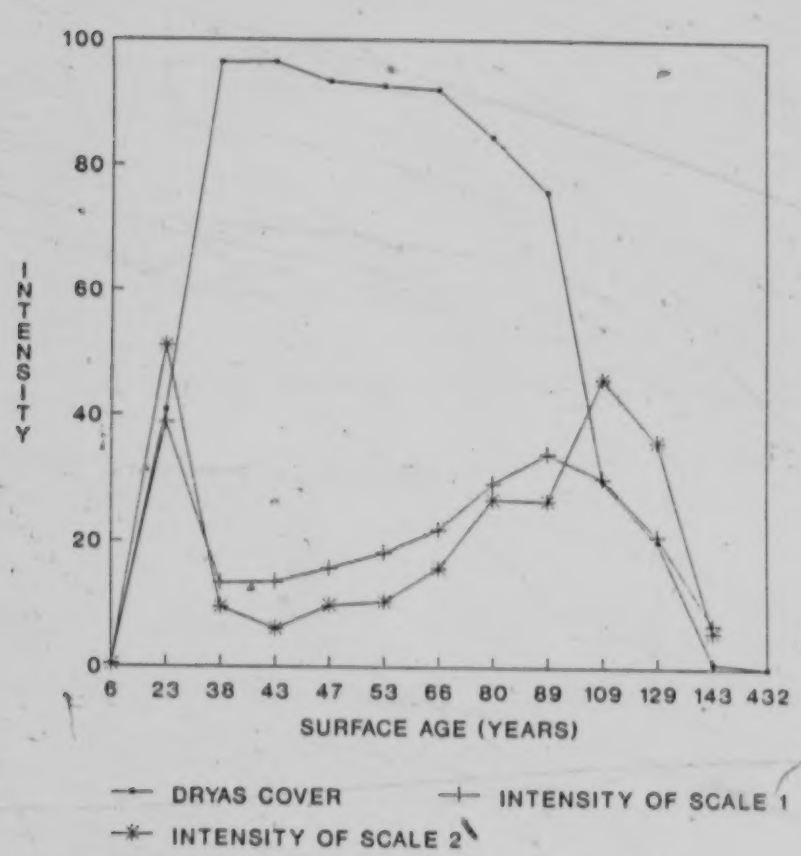
cover was higher in the old channel bottoms, and as described before, always established first along channel margins. This phenomenon was observed on other proglacial landscapes in the region (e.g., Saskatchewan Glacier forefield).

2.4.2.2 Southeast Lyell Glacier Site

It is harder to draw general conclusions for the four species groups at the Southeast Lyell site due to a much greater floristic and physiognomic complexity. High surface and micro-habitat heterogeneity leads to community and pattern complexity. Much of the spatial pattern could be due to biotic and environmental interactions and underlying environmental controls at numerous scales. The relative effects of these factors on small-scale species patterns is hard to separate (Galiano 1985). Although some researchers recommend sampling the individual factors (e.g., Castro et al. 1986), this was not done, so only broad ecological conclusions can be drawn.

The Southeast Lyell site has the complete sequence of pattern development for *Dryas* as envisaged by Greig-Smith's model. Indeed, it is the only species group to show the full cycle from establishment to eventual disappearance from the community. Initially, *Dryas* seeds germinate in a pattern which is determined by the heterogeneity of the substrate surface (Harper et al. 1969). The initial *Dryas* pattern has low intensity, small patch size and a scale determined by initial spacing of seedlings. As the *Dryas* clones grow and coalesce, patch size increases, intensity increases and then decreases, although, due to infilling, the smallest scale of pattern does not disappear. Up to this point, the *Dryas* development is similar to that at the Icefield, but then as the shade-intolerant *Dryas* senesces, its pattern development is reversed. Along with a decrease in patch size, there is a second increase in intensity (and subsequent decline) as the patches start to decay and the total cover is reduced (Table 2-5 and Figure 2-8). As the *Dryas* disappears from the community, intensity declines to near zero.

Figure 2-8 Pattern Intensity for *Dryas drummondii*, Southeast Lyell Glacier Site



Two Smallest Scale Patterns
Dryas cover includes both live and dead.
Each point is from 2 transect average.

McDonough (1965) describes the same trend during cactus senescence in a desert habitat.

Dryas pattern scale is not really constant at the Southeast Lyell site (Table 2-5). The *Dryas* development appeared more variable than at the Icefield site. Even on 40-year-old surfaces, *Dryas* cover ranged from 0 to 100 %. This was mostly in areas of bedrock exposure, excess soil moisture or highly exposed or unstable areas. As with the conifers, there may be infilling on the older surfaces, so there is not a single cohort. As well, the surface is much less uniform than at the Icefield sites (both in terms of topography and material), and so a constant environmental grain cannot be assumed. The *Dryas* develops best on large gravels and cobbles because there is adequate stability while there are available fines between the cracks.

Dryas disappears from the later Southeast Lyell seral communities for two reasons: (1) It is very shade intolerant (Watson et al. 1980), so once the overstorey develops, the *Dryas* cannot regenerate (greatly reduced vigour was noted in more shady areas). A secondary effect of conifer development is the influence of needle shedding on *Dryas*, a calciphile; the pH declines rapidly in litter horizons with high needle content (see section 1.3.7). (2) *Dryas* requires a mineral substrate (specifically well-drained gravels; it won't grow in silty areas) for colonization, and will not become established by seed on organic matter (Anderson 1967a). Unlike the Icefield environment, the duff layer becomes permanently established, due to a less windy microclimate, better vegetation establishment and more stable surfaces. *Dryas* can only re-colonize organic surfaces by expansion from existing adjacent clones. On the older surfaces, the only bare mineral soil was along the more exposed moraine crests (always composed of finer-textured material), especially on the south side of the river. Here, *Dryas* is continually re-invading the more exposed moraine crests and is periodically "driven back" by episodes of increased climatic severity and surface instability. In this instance, *Dryas* development is not always uni-

directional, even at the Southeast Lyell site.

Pattern trends in the non-vascular plants may have an ecological explanation (Table 2-6). Pattern scale is less constant than for conifers. This is not surprising since, unlike conifers, field observations indicate that patch growth is due more to infilling than radial expansion of existing individuals. This conclusion is supported by the patch-gap analysis. On intermediate surfaces, scale decreases, due to a decrease in gap size. At this stage, the mosses are starting to colonize the dead *Dryas* centres resulting in numerous small moss patches. On older surfaces the scale and gap size increases (Table 2-6) because, although the sites are more shady, the greater shrub cover (especially *Shepherdia*) with its high litter production (Crocker and Major 1955) results in large areas not suitable for moss development. The mossy patches do not start to coalesce until the old-growth forest stage, which has a lower shrub cover. The high moss cover (60%) is typical for this *Picea engelmannii-Abies lasiocarpa* forest type which supports the most extensive bryophyte communities within the region (Lee and La Roi 1978). On this site, non-vascular patch size increases (although scale only increases slightly). This is due to large uniform patches of moss interspersed with more open less mossy areas, which are a function of canopy openings due to treefall (tree gap dynamics).

The trend in number of pattern scales at the Southeast Lyell site supports the hypothesis that maximum pattern diversity occurs on intermediate-aged surfaces. All the following species groups had a maximum number (range 5-7) of scales of pattern (initial uncorrected peaks in TTLQV variance plots) at the following ages: *Dryas*: 47 years, conifers: 43 years, non-vasculars: 80 years, and shrubs: 90 years. The time of maximum peak for each species group was the same even after the peak correction technique (Dale and MacIsaac 1989) was applied. This seems to follow the successional sequence for each group except for conifers. On the early *Dryas*-dominated seral stages, and in the old-growth forest, the overall pattern diversity probably decreased due to

greater dominance by one or two species groups.

Pattern intensity for the different species groups is related to growth-form. Since crown cover, rather than shoot cover was recorded, tree cover in quadrats was often either 0% or 100%. Smaller plants often had a wider variety of cover values in the adjacent quadrats. This is why conifers had higher maximum intensity values and non-vascular plants and *Dryas* had lower maximum intensity.

As with many deglaciated sites (e.g., Matthews 1978) and other early successional environments (Sterling et al. 1984), the pioneer vegetation is very heterogeneous. This is usually related to microscale variations in relief, moisture and texture. Theakstone and Knighton (1979) have reported that even old caribou hoof prints on glacial debris affect subsequent vegetation distribution. As the *Dryas* cover becomes ubiquitous, this fine grain heterogeneity quickly disappears, usually within 50 years (Crocker and Major 1955). This meso-scale pattern variation is mostly related to slope aspect, increases until canopy closure around 100 years. By that time tree gap dynamics are contributing to new patchiness.

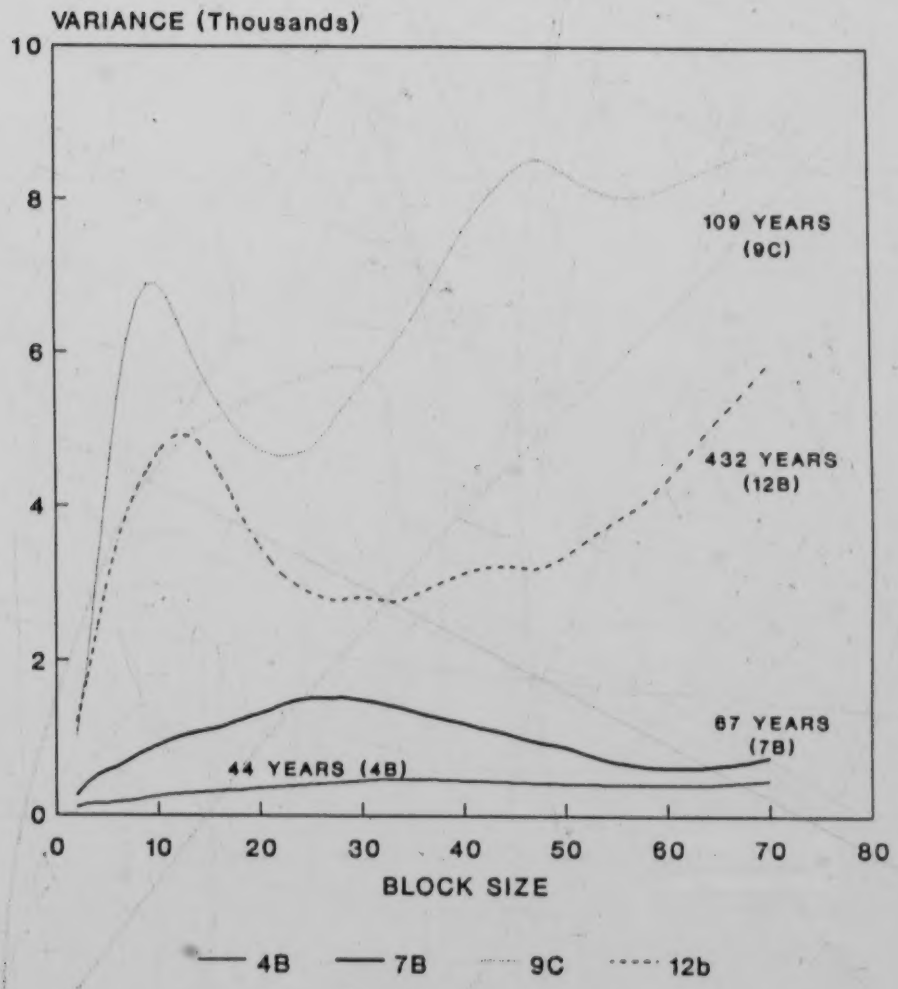
The overall development of pattern for the persistent species groups at the Southeast Lyell site does, to some extent, follow the sequence outlined by Greig-Smith and expanded by Yarranton and Morrison's two stage pattern development model as shown in Figure 2-3. The pattern development of the persistent species mirrors that of the colonizing *Dryas*, although the former groups do not exhibit the senescence phase (and associated pattern changes) as does the latter. The scale of some species groups does remain constant throughout the successional sequence, while for other species groups, there is a gradual increase. Intensity is at a maximum just before the patches coalesce (as predicted). Patch size does increase with age, but, a clear pattern is not detected for all species groups. A series of TTLQV curves (before peak correction) for the shrub species group on different surfaces is

presented in Figure 2-9. It illustrates the changes in intensity (as shown by variance) and the relatively constant scale during the succession. Earlier authors (e.g., Usher 1983) indicated a trend for variance to increase for increasing block size. In contrast, Dale and MacIsaac's (1989) methods usually detect highest intensity at smallest scales (for all species at all study sites). This is logical, as at this scale, the pattern is less likely to be interrupted, and this concurs with Greig-Smith's (1964) original hypothesis.

If the facilitation model (Connell and Slatyer 1977) describes this succession, one would expect pattern scale to be equal for colonizing and persistent species because the persistent species would initially establish where the colonizers started out, as is found in some studies (e.g., Yarranton and Morrison 1974) and shown in Figure 2-3. As the colonizing taxon declined, its patch size and intensity would decrease. Although the initial scales of pattern for all species are all within a 1 to 2 m range (Tables 2-5 to 2-8), it would be difficult to determine whether this is in fact happening. As mentioned above, the pattern trends for the colonizing species (*Dryas*) is consistent with the model.

In addition to individual species pattern, Greig-Smith (1964) also relates overall pattern to concepts of climax and succession. In early seral vegetation, some species will be growing with optimal conditions (and exhibit maximum scale and minimum intensity). There will be other invading species, however, which show more intense and smaller scale pattern, so that the overall scale of pattern will be less, and the intensity greater, than in a seral climax community. If this model is correct, then the average scale and intensity for the four species groups should be maximized and minimized, respectively, in the climax forest. In the old growth forest, while average intensity is lower than on younger surfaces, average scale is not at a maximum for the chronosequence (Tables 2-5 to 2-8). This may be because, except for *Dryas drummondii*, the pattern analysis was conducted on species groups, rather than individual species.

Figure 2-9 TTLQV Variance Plots for Shrub Species, Southeast Lyell Glacier Site



Original results before peak correction.
Does not include Dryas drummondii.

2.4.2.3 General Discussion

A comparison of *Dryas* pattern development between the Sunwapta and Southeast Lyell chronosequences does yield interesting results (Tables 2-2 to 2-5). The relationship between cover and intensity follows the trends predicted in the Greig-Smith model. At the Sunwapta site, the intensity increases in conjunction with cover and reaches a maximum at 30 years where cover is around 50% (Table 2-2). As expected, it does decline as the *Dryas* cover continues to increase (patches coalesce). Because the *Dryas* cover reaches a steady value on the older surfaces, and does not reach 100% cover (or show a subsequent decline and disappearance from the community) the latter part of Greig-Smith's pattern development is not represented.

The effect of environment on pattern development is very apparent by comparison of the two very different systems. At the Icefield site, abiotic factors continue to "entrain" the pattern, even after 110 years. At the Southeast Lyell site, biotic factors dominate in the older seral stages and in the climax forest. In the old-growth forest, the large-scale patterns of conifers, shrubs and non-vascular plants appear to be mainly controlled by canopy openings created by treefalls. This phenomenon, which is important in old-growth forests (Veblen 1986) causes variability in understorey light profiles which significantly affects understorey pattern (Ross et al. 1986). This is not related to original environmental grain, but is a function of tree gap dynamics.

Simple communities dominated by *Dryas drummondii* and *D. integrifolia* occur on river flats in lower sub-alpine elevations throughout the study area (including downvalley from the Southeast Lyell site) (Walker et al. 1982). These early-successional communities are not replaced by later seral stages because of periodic river flooding (in contrast to the Icefield site, where climate is the controlling factor). Although superficially similar vegetation at the Icefield site, they are often much wetter, and if not disturbed, will develop to a *Salix* or open

Picea-dominated community (Walker et al. 1982, p. 392).

Why *Dryas* decays in the open environments at the Icefield and Southeast Lyell sites is unanswered. It may be due to climatic variation which results in periodically unfavourable growing conditions. Pathogenic fungi may also have an influence. *Marasmius epidryas* (although not confirmed as pathogenic) was widespread on dead *Dryas* tissue at the Icefield. Sprauge and Lawrence (1960) and Lawrence et al. (1967) note this species along with *M. fuscopurpureus* Fr. and *Helotium scutula* (Pers.) Karst. on dead *Dryas* tissue on young post-glacial surfaces in southeast Alaska. Tisdale et al. (1966) reported that *Dryas* cover decreased over a 30 year period on open outwash at Kinney Lake near Mt. Robson. At the Southeast Lyell site, older clones were less vigorous (browner leaves, fewer flowers) especially in sites with some overstorey shading. Experimental research is needed to discern the actual causes of *Dryas* mortality.

Pattern scale (particularly larger scale) is not the same on the different-aged surfaces, particularly at the Southeast Lyell site. This variation in scale may have two sources. First, the assumption that all the sites along a specific chronosequence have the same environmental grain is probably invalid. The grain is quite variable, even in the superficially homogeneous Icefield sites, due to variations in microsite, topography and aspect. Second, there is evidence that after a species does establish, there is infilling by later recruitment. Although most trees on a specific surface at the Southeast Lyell site were probably from a single cohort (shown by even size), there was some post-establishment infilling, especially on old surfaces (in the old-growth forest it is obvious). Evidence includes a lack of a decrease the cover of small-sized conifers with time ($P < .05$), and that on all the transects, most of the variance peaks for conifers were ranged from 1-3 m. There is substantial cone production on most the *Picea* on surfaces older than 55 years, which provides a local seed source. This infilling may be a factor (along with tree growth) in increases in scale (Table

2-8). For all species groups, there is an increase in the smallest scale of pattern over time, with peak values on the 90 to 140-year-old surfaces.

As with other studies (e.g., Galiano 1983), at least two scales of pattern can be seen on most of the transects at both study sites. The controls on small scale pattern are complex, although they appear to be mostly due to plant morphology (e.g., average size and growth of individuals). Castro et al. (1986) and Sterling et al. (1984) report that in Mediterranean pastures, the fine-grained pattern is mainly due to microrelief. Galiano (1983) and Usher (1983), using association analysis, conclude that small scale variation may be due to interspecific interactions such as species exclusion. All these factors are probably important. A possible example of competitive exclusion is the development of mossy areas in the centre of old *Dryas* clones. It is not known if the mosses are excluded until the *Dryas* decays, and if, once the mosses develop, they exclude subsequent *Dryas* regeneration.

The larger scales (sometimes more than one in a transect) are related to environmental controls (i.e., discontinuities and gradients) as described by Kershaw (1963, 1973) and Galiano (1985). As also reported by Galiano (1986), these larger scale patterns are more variable, which is expected, given the greater variation in environmental factors, as compared to morphological ones. They can be harder to detect than the smaller scale patterns. Aspect has a major influence on larger scale pattern on the bigger, more hummocky older moraines at the Southeast Lyell site. Although the 90 m transects were mostly on southwest-facing slopes, due to the hummocky nature of the moraines, they also crossed some concave and north- to east-facing slopes. Conifer, shrub and moss density was higher on these surfaces, and the scale over 10 m may reflect their distribution.

There is no evidence, however, for Kershaw's (1973) sociologically-imposed pattern which supposedly operates at a scale intermediate to the

ones described above and which is related to methods of dispersal and regeneration. Greig-Smith (1961) states that development of a clumped pattern by successive generations establishing around pioneer individuals is probably rare, because seed dispersal usually efficiently covers a much wider area. This is undoubtedly the case at the study sites. For the major species, such as *Dryas drummondii*, close proximity of seed source results in a good seed rain on all surfaces (Heusser 1956) so that patches do not increase cover by outward expansion of successive generations as noted in some sand dune successions. To investigate the underlying environmental associations, one should measure environmental attributes at the same scale as the pattern analysis (Gibson and Greig-Smith 1986). Causal mechanisms cannot be tested using this observational approach: a more structure experimental design is required (Harper 1982).

Often the dominant species can control the temporal dynamics and spatial structure of the whole community (Watt 1947a, Greig-Smith 1979), because its occupation of a surface alters the substrate, making it heterogeneous for other species (Galiano 1986). Although *Dryas drummondii* plays a major role early in the successions included in this study (an almost exclusive role at the Icefield site), it does not appear to control subsequent community development. This may be due to two factors. First, it is a short-lived species (Wilson 1978). In the 80 years in which it dominates at the Southeast Lyell site, it probably does not affect the substrate sufficiently to entrain the pattern of subsequent vegetation. Second, it attains almost 100% cover, so it modifies the substrate everywhere and may not cause significant microsite variation.

While general conclusions can be drawn, one of the difficulties of pattern analysis is the wide variety of alternative hypotheses to the null hypothesis (the null hypothesis is that there is no pattern) (Bouxin and Gautier 1982). Kershaw (1973) states that complexity and variations in distribution of individuals is such that formulation of a

model is almost impossible. As well, interpretation of data from multiple scale pattern may be very difficult (Errington 1973).

2.4.2.4 Methodology

There are many methodological factors (in addition to biological or environmental ones) which may affect the pattern analysis results and interpretation. The results of the runs test can be affected by relationship between the quadrat size and individual plant size (M. Dale pers. comm.). For all species groups, the 30 cm quadrats are smaller than the average vascular plant size (except on very young surfaces). The only exception is with the non-vascular species group. In the latter case, the probability of concluding that patches are present is increased because of an increase in runs of sparse quadrats.

The length of the transect is another factor to consider. A long run of contiguous quadrats is needed to detect larger scale patterns. For example, at a block size of 75 (22.5 m), the variance is calculated on 151 quadrat block pairs (each pair is 150 quadrats long). There is only one degree of freedom for pattern at that scale, since there are only two independent (totally non-overlapping) comparisons in the transect of 300 quadrats. Larger quadrats aligned along a longer transect might be a better approach to analyze pattern with trees and shrubs. Conversely, smaller quadrats might be more suitable for non-vascular plant analysis. The size of the quadrats can affect the interpretation of pattern analysis (Usher 1983), although it is not as important as the transect length. Most other studies (in grasslands) use smaller quadrats (e.g., 10 cm x 10 cm Castro et al. 1986, Galiano 1986) and they are a better size for detailed measurement of soil parameters for correlation analysis.

The patch and gap results do not exhibit good discrimination, although the detection of patch and gap is best when *Dryas* or the species group has cover around 50 %. Even in cases of uniform scale,

there are variations in patch and gap size within and between transects on similar-aged surfaces. This is because of ongoing recruitment of *Dryas* and the patchy nature of its decay, both resulting in irregular (different sized) patches and gaps (Figure 2-2). Dale and MacIsaac (1989) suggest using running averages of two or three quadrats (effectively increasing quadrat size) to reduce the effect of this small-scale irregular pattern caused by clonal decay. Dale and Blundon (*in press*) discuss problems with pattern irregularity in general, and propose more elegant methods to cope with it in pattern analysis.

Once a pattern analysis method is widely publicized, there is a tendency to use it uncritically. This may explain the recent use of the BQV method when other better methods are available (see Ismail and Babikir 1986). Likewise with these methods described above. Even though they may be useful, they have to be examined in a critical light before they are accepted. If not, they may lead to erroneous conclusions of pattern analysis (for an example, see the criticism of Galiano's (1982a) "New Local Quadrat Variance" method by Dale and MacIsaac (1989)).

Many of these methods provide imprecise results; some results may be as much a function of methodological influences as biological or environmental ones. While the accuracy may be suspect, the general story from an ecological perspective is rather more clear; in any case the inaccuracies may not be of ecological importance (Dale and MacIsaac 1989). One approach to reduce spurious results and interpretations is to lump data from several transects sampled in a belt (Usher 1983). Ongoing refinement of these methods, especially the newer ones (Dale and MacIsaac 1989) is needed (e.g., see Dale and Blundon *in press*), and they have to be tested in a variety of vegetation types before they can be generally accepted. There is evidence that they are not well suited for more complex systems such as at the Southeast Lyell site, but more simple ones such as at the Columbia Icefield. Once they are accepted, the results from them may greatly add to the understanding of pattern dynamics in primary succession. While these results provide useful

descriptive information, by themselves they are not adequate to test the cause of pattern. This requires geographically-referenced environmental data and enumeration of all individuals in a sample sub-population (Franklin et al. 1985). A final warning may be taken from Tansley (1920 cf. Franklin et al. 1985): mathematical models which are sufficiently complex to describe the spatial patterns completely, may be too restrictive in their underlying assumptions to be applicable to highly variable natural patterns.

Goodall (1974) and Kershaw (1970) caution that because contiguous quadrat methods are based on the underlying assumption of a continuous distribution, they should not be used where there is low overall cover (zero density in many quadrats) in which there is very marked but scattered clumping. Errington (1973) likewise states that interpretation of pattern data from quadrats having less than 10% or greater than 90% cover is difficult. This could account for the best results being attained when cover is 50%. It may be that the use of a single set of pattern analysis methods for the whole chronosequence (which may include very high and very low densities for a particular species) may not be advisable. An alternate approach would be to convert abundance data to presence-absence data and use other techniques cutlined by Pielou (1977).

2.5 Conclusions

This research had two major purposes: (1) Testing and validation with field data newly developed contiguous quadrat methods of pattern intensity and pattern patch/gap analysis. (2) Elucidation of the successional pattern dynamics of two very different chronosequences.

Spatial plant pattern development during primary succession has been described for two different, recently deglaciated environments. *Dryas drummondii* plays a major role in the pattern development at both study

sites. At the Columbia Icefield, the successional pathway and pattern development is cyclical, whereas, at the Southeast Lyell it proceeds in one direction and it is more complex (i.e., has more species groups). At the Icefield site, only a *Dryas*-dominated community is present. Early pattern development is similar to the Southeast Lyell site, except that as the *Dryas* clones die of old age they are not replaced by longer-lived woody plants, but rather by a cyclical replacement of *Dryas* seedlings.

All the species which dominate in communities on older moraines at the Southeast Lyell site are present at the Icefield site as well (*Abies lasiocarpa*, *Picea engelmannii*, *Shepherdia canadensis*, *Salix glauca* var *villosa* and mosses). The divergence in pattern development is probably due to climatic differences between these two sites (one lower subalpine, the other upper subalpine).

Environment plays a major role in successional dynamics and the influence of microsite heterogeneity cannot be overstated (i.e., influence on colonization and growth). Even in apparently homogeneous sites, environmental heterogeneity is important. Morphological control, however, is still most important in explaining pattern development (e.g., establishment and growth of clones and patches).

There is some evidence for nucleation by *Dryas drummondii* and its role in quantitative facilitation during succession. Most of the evidence suggests, however, that surface stability (autogenic control) is the major factor in establishment of *Dryas* and longer-lived species.

The model of pattern development as proposed by Greig-Smith and modified by Yarranton and Morrison does appear to explain the observed changes in pattern during primary succession, especially in the simple *Dryas*-dominated systems. It is much harder to draw general conclusions at the Southeast Lyell site, with greater physiognomic, floristic and microsite complexity. Much of the pattern could be due to biotic interactions and environmental factors operating at several levels.

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3 PRIMARY SUCCESSION ON PROGLACIAL MORAINES AT THE SOUTHEAST LYELL GLACIER, ALBERTA

3.1 Introduction

There are two main approaches to successional studies: static and dynamic (Austin 1977). The static approach includes a spatial gradient to simulate a temporal gradient, and involves several observations taken at one time. It was the approach used in this research. This succession research is useful for drawing generalizations about changes in certain community parameters (e.g., diversity) over time (Whittaker 1975, p.181).

Studies of primary plant succession on proglacial deposits (e.g., Cooper 1939, Scott 1974) have had a major influence on the development of theories of succession in the past 70 years. Many studies have been done on the early successional plant communities on proglacial deposits in coastal Alaska (Cooper 1923, 1931, 1939; Decker 1966, Reiners et al. 1971) and to a lesser extent in the interior of the state (Viereck 1970, Scott 1974). In the Canadian Rockies, most of the publications are from studies on the Mount Robson moraines, 210 km to the northwest (e.g., Cooper 1916, Tisdale et al. 1966, Sondheim and Standish 1983 and Blundon 1989). The only previous vegetation studies at the Southeast Lyell Glacier were brief descriptions published by Heusser (1956) and Walker et al. (1982, p. 511).

Reiners et al. (1971) and other workers have noted that the influence of *Dryas* and other early-successional species on the rate and pathway of primary succession can vary from region to region, due to different abiotic influences and species assemblages in the early seral stages. This limits our ability to extrapolate from one study to other areas. In Alaskan coastal sites, *Alnus crispa* is a very important species in the successional sequence (Lawrence 1958, Lawrence et al. 1967). Although present in the Canadian Rockies, this species appears to

be absent from glacier forefields (Heusser 1956). This kind of difference is one reason for repeating this sort of research, even though it has been done in similar environments elsewhere.

A second reason for this research is that the successional sequence at the Southeast Lyell study site allows successional theory to be tested. For example, Odum (1969) suggested that during any plant succession, the organisms themselves modify and gain control over the environment (autogenic succession). As well, he suggested that species diversity (both richness and equitability) is low in early stages and reaches a maximum in mature stages. As well, spatial heterogeneity (vegetation pattern diversity) is poorly organized in early stages and well organized in mature stages. These hypotheses can be tested at this site.

In examining the primary succession on proglacial moraines, the following approach was used. First, determine what are the plant community attributes of interest. Second, determine how these attributes change over time. Based on the second part, the third task is to discern what the controls are on this change. Why do these plant community attributes change over time? These three questions are answered, in turn, in the Introduction, Results and Discussion sections of this paper.

To answer the general question "how do the plant community attributes change over time?", the following eight specific questions (based on the general literature) are asked (see also Discussion):

1. Can distinct seral stages or communities be recognized along the time gradient?
2. When is the vegetation mosaic of community types most diverse?
3. When is plant diversity within a single community most diverse?
4. Is the rate of change over time constant?
5. Does the non-vascular plant development mirror the vascular plant development?

6. Does community development proceed in a unidirectional manner (i.e., are the trends monotonic)?
7. Are there environmental gradients, besides the time gradient, that are influencing the succession?
8. Does the succession documented in this thesis constitute a typical example of primary succession for comparable proglacial sites in the study region? How does it compare with succession in similar environments in other regions?

3.1.1 Research Objective and Hypotheses

The major objective was to describe the process and determine the rate of plant community development during primary succession on proglacial moraines of known ages in the Canadian Rocky Mountains.

The hypothesis tested is as follows:

Primary plant succession (community development) on proglacial deposits proceeds in a unidirectional, predictable manner; floristically, structurally and in terms of diversity. The development of the plant communities varies most along the fourth dimension, which is time, as expressed by distance from the glacier.

This general hypothesis can be expressed in the following specific hypotheses (some of which are derived from Odum (1969)):

a) Species diversity and richness will increase during the early stages of the succession as increasingly greater numbers of species are recruited during the development of the early seral stages.

b) Maximum diversity will occur on the intermediate-aged moraines

where early and late successional species co-exist.

c) Dominance concentration will decrease over time, as dominance by early colonizers such as *Dryas drummondii* decrease and as species richness increases.

3.2 Methods

3.2.1 Field Methods

Community analysis was performed at the Southeast Lyell site. Field work was conducted during the period June 30th to August 10th, 1984. The vegetation sampling was done along the same transects used for the plant pattern research (Section 2.2.1 for location of transects and other information). Pattern analysis transect 9C was not sampled, however, because it was not paired with a second transect on a similar-aged surface.

For the purpose of vegetation sampling, a stratified random method was used (Mueller-Dombois and Ellenberg 1974, p. 39) in which the 90 m long pattern transects were divided into thirds, giving 72 "plots" in total along the 24 transects. A species-area curve (vascular and non-vascular) was developed for each pair of 90-m long transects to determine the minimum sample size (i.e, quadrat area) needed for each stratum sampled at that location (Mueller-Dombois and Ellenberg 1974, p.48).

Plant crown cover[1] in the lowest stratum from 0-0.5 m (herbs, non-vascular species, prostrate and low shrubs) was estimated for each macroscopic species by combining the data collected from the 100 0.3 x

[1] Using the same definition of "crown cover" used in the pattern research (see Section 2.2.1 for details).

0.3 m contiguous quadrats along that portion of the transect. This totalled 27 m^2 of area, which was more than the minimum area required in all cases (based on the species-area curves).

To estimate crown cover of woody plants in the layers above 0.5 m, one nested quadrat was randomly placed along the 30 transect segment (3 nested quadrats per transect). Plant cover was estimated for each species in each of the following strata: 0.5 - 2.0 m (medium shrub); 2.0 - 5.0 m (tall shrub) and > 5.0 m (tree). The following quadrat sizes were used: 2 x 2 m, 5 x 5 m and 6 x 6 m for the medium shrub, tall shrub and tree strata, respectively. The 5 x 5 m plot was nested in a randomly-chosen corner of the 6 x 6 m plot. A 2 x 2 m plot was nested in each of the four corners of the 5 x 5 m plot (four 2 x 2 m plots in total). Species-area curves indicated that at least 16m^2 was required to adequately sample the medium shrub stratum. Species cover in this stratum was estimated using the four smaller quadrats (2 x 2 m) rather than one large 4 x 4 m quadrat, since the smaller quadrats appeared to be most appropriate in relation to the size of the shrubs. The nested quadrat design described above was used for sampling on all transects, because, in all cases, it was determined from species-area curves that they provided adequate sampling coverage. These were the same plots used in the height-class determination described in section 2.2.1.

Voucher specimens were collected from any plot for unknown species. In addition, a general collection was made for all species for verification. A species-presence list was compiled from all plants found within the glacial trimline and in the old growth forest within 50 m of transects 12A and 12B (Appendix 3-6). Voucher specimens of the vascular species are deposited in the University of Alberta vascular herbarium (ALTA), Edmonton, Canada.

3.2.2 Data Analysis Methods

For the purpose of analysis and discussion, each 30 m transect

section (and its associated nested quadrat) were considered as a sample "plot". Six of these grouped together (comprising a transect pair e.g., 10A and 10B) would represent a "stand", whereas the five groups of transects would represent plant communities, or seral stages in the succession. Analysis was based on different groupings of plots, depending on the objective. For summary purposes, the five seral stage groups were used (from 6 to 24 plots in each). Trends which were shown graphically were based on grouping the 12 transect pairs (6 plots each).

A series of multivariate analysis techniques were used on the data. As Austin (1977) states, they are useful for summarizing successional data and are often under-utilized in this type of research. To classify the plots into seral stages and to detect associations in the data, a cluster analysis (CLUSTAN) and a two-way indicator species analysis (TWINSPAN) were conducted using the CLUSTAN (Wishart 1987) and the TWINSPAN (Hill 1979b) computer packages.

The cluster analysis method used a sequential, agglomerative, hierarchical and non-overlapping (SAHN) classification of the 24 transects (3 plots each) using polythetic criteria (species abundance data). Cluster fusions were calculated using the "unweighted group averaging clustering" method (Pielou 1984, p. 73). It is the most frequently used classification method (Sneath and Sokal 1973) and is recommended when there is no specific reason to choose another hierarchical technique (Gauch 1982). This method has several advantageous characteristics such as preservation of space (Sneath and Sokal 1973) and no dendrogram reversals (Pielou 1984, p. 75). The similarity matrix computed for the 24 stands used the Similarity Ratio, which is an abundance analogue to Jaccard's Index (Wishart 1987).

TWINSPAN is a complex method in which ordination and classification (polythetic, divisive) are done simultaneously (Pielou 1984, p. 220). In an iterative process, the plots (individuals) are classified first using one-dimensional reciprocal averaging (RA), and the species (attributes)

are classified second using the plot classification as a basis. TWINSPAN analysis was used to produce an ordered species-stand table which is similar to Braun-Blanquet's Tabular Classification method (Hill 1979b). As well, the resultant plot hierarchy was used to create a dendrogram with the sequences of divisions as integral levels (Gauch 1982, p. 201). This dendrogram is arranged by TWINSPAN with the similar plots located close to each other (Pielou 1984, p. 220), so that there are no "dendrogram reversals" as with CLUSTAN. The default settings were used except for the pseudo-species cut-off levels which were: 0.0 0.5 1.0 5.0 10.0 and 25.0 % cover. As well, the minimum group size for division was set to three.

The plots were ordinated using Detrended Correspondence Analysis (DCA), which is a detrended form of reciprocal averaging (RA) (Hill and Gauch 1980), using the DECORANA computer program (Hill 1979a). This metric multidimensional scaling technique gives a better representation of the interrelationships of the data than either ordinary RA or Principal Components Analysis (PCA) (Pielou 1984, p.195). It overcomes the two main faults of RA by flattening out the arch distortion of the second and higher axes and correcting the scale contraction at the ends of the data swarm (Gauch 1982, p. 153). The distortion caused by gradients in beta diversity and species richness are largely removed with DECORANA (Dargie 1986). DCA is complementary to TWINSPAN because, among other things, the axes are independent (Gaugh 1982, p. 203). It has been recommended by Kenkel and Orloci (1986) as being a robust metric method although it is best done in conjunction with RA analysis to determine the effect of the detrending on the specific data set. The following options were used: data not transformed, rare species not downweighted, axes re-scaled. All other options were set to default.

Statistical analysis was performed on the data grouped into the five seral stages identified by the CLUSTAN and TWINSPAN analyses. To show trends it was also done on the 12 transect pairs. USER1, a user-written SPSSx procedure was used for the analysis (SPSS Inc. 1983, Lee 1984).

This package produced the following analyses calculated for each "group" based on cover estimates:

1. Species Structure Curves. These are the same as Whittaker's (1965) Dominance-Diversity Curves, except that species names are plotted on the curve beside their respective position. These were constructed for each stand and then compared in terms of species sequences and shape.

2. Simpson's Index of Dominance Concentration (Equitability) (C) (Simpson 1949 cf. Whittaker 1975, p. 95). The equation is as follows:

$$C = \sum_{i=1}^{s} [n_i/N]^2 = \sum_{i=1}^{s} p_i^2 \quad \text{(simplified form on right)}$$

where s is the number of species in the sample, N the total of all species abundances ("importance"), n_i the abundance for the ith species, and p_i the relative abundance (expressed as decimal fraction) of the ith species. C can have values between 0 to 1.

3. Shannon-Weaver Index of Diversity (H') (Shannon and Weaver 1949 cf. Whittaker 1975, p. 95). The equation (which can also be calculated for $\log_{10}$) is as follows:

$$H' = -\sum_{i=1}^{s} [n_i/N] \log_e [n_i/N] = -\sum_{i=1}^{s} p_i \log_e p_i \quad \text{(simplified form on right)}$$

The symbols have the same meaning as defined for Simpson's index. This equation is composed of additive terms (Pielou 1977, p. 311), of which only the first term (shown above) is used in the calculation. This creates a slight bias which overestimates H'.

4. Descriptive statistics for each variable (frequency, mean, standard error of the mean).

The Simpson index and Shannon-Weaver index are closely related (Pielou 1977, p. 311). They are equitability indices which are measures of the variation in the proportions among species. The Simpson index is most sensitive to the numbers of abundant species and gives little weight to rare species. The Shannon-Weaver index is more sensitive to rare species and, therefore, is more adversely affected by sampling error.

Evenness (E), which compares observed diversity with potential maximum diversity, was also calculated, using the following equation from Pielou (1977, p. 307):

$E = H'/H_{max}$ where $H_{max} = \log_e s$ (s is the total number of species).

This measure is susceptible to sample error because H_{max} gives as much weight to observations of rare species as to observations of common ones (Pielou 1977, p. 309). In this research, this error is probably low because of the intensive sample method used for species under 0.5 m (which would be the ones most likely overlooked).

The plant community analysis results were subjected to standard non-parametric statistical analysis. To test for correlations between vegetation attributes and time, Kendall's correlation coefficient was used (Sokal and Rohlf 1981, p.602). The Mann-Whitney U test was used to test for significant differences in mean values on different-aged surfaces (Sokal and Rohlf 1981, p.433).

To compare and contrast plant community development for the vascular species and non-vascular species component, the multivariate and statistical analysis described above were performed on these two groups separately, as well as on total species combined.

3.3 Results

Based on the TWINSPAN classification at the five-cluster level (using all species), the successional sequence at the Southeast Lyell site can be divided into five seral stages (Figure 3-1), corresponding to the following surface ages: Stage 1: 0-20 years (Transects 1A and 1B); Stage 2: 20-50 years (2A to 5B); Stage 3: 50-90 years (6A to 9B); Stage 4: 125-145 years (10A to 11B); Stage 5: > 432 years (12A and 12B). The TWINSPAN species-stand tables (Tables 3-1 and 3-2), clearly show the shift in early vs. late successional species (see Discussion). The TWINSPAN classification is generally supported by the CLUSTAN cluster analyses based on all species and on vascular species (Figure 3-2, parts a and b); the major difference is that the CLUSTAN division between seral stages 2 and 3 is not clearly defined. The CLUSTAN classification using only non-vascular species, gives slightly different results, with more distinct clusters on the young surfaces (Figure 3-2, part c).

The ordination diagrams can be viewed in two ways: the spatial representation of the data points (Matthews 1979) and, as Wilson (1981) explains, the actual "percentage variance explained" by each ordination axis. The DECORANA results for total species support the classification scheme. The 24 "stands" (based on 3 plot groups along each transect) are grouped into the five seral stages along the first axis, which is time (Figures 3-3). Time is significantly correlated ($P < .001$) with stand position along the first axis. The ordination diagram based on vascular species (not shown) is very similar to the ordination based on all species, which reflects the dominance of the vascular species in the overall community development. The non-vascular species ordination (Figure 3-4) is less clear, but does show an obvious distribution over time as axis 1. Time is significantly correlated ($P < .01$) with stand position along the first axis. In all three ordinations discussed above, change in time (first axis) explains over 80% of the observed

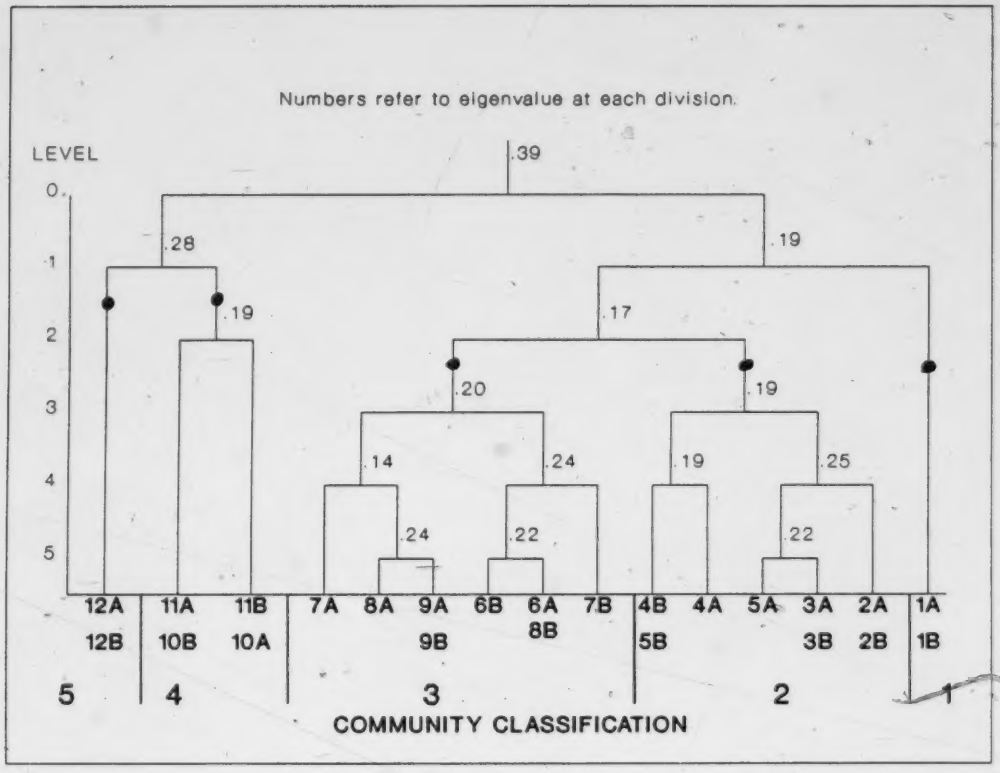

Numbers refer to eigenvalue at each division.
LEVEL
0
1
2
3
4
5
.39
.28
.19
.19
.17
.20
.19
.14
.24
.19
.25
.24
.22
.22
12A
12B
11A
10B
11B
10A
7A
8A
9A
9B
6B
6A
8B
7B
4B
5B
4A
5A
3A
3B
2A
2B
1A
1B
5
4
3
2
1
COMMUNITY CLASSIFICATION

Table 3-1 TWINSPAN Species-Stand Table for Southeast Lyell Site Vascular Species, 24 Stands[1]

STAND ORDER

22221211111111 1
34019236782154807956341 2

SPECIES ORDER

		SPECIES CLASSIFICATION
PYAS	321113--1--111--1-------	11111
POBA	642433--1--1-1--1111----	11111
DECA	1-----------------------	111011
CAEB	12----------------------	111011
OSDE	1-----------------------	111011
HAOB	11----------------------	111011
ARRU	31---3------------------	111010
CHUM	2111-1--1---------------	111001
CAAU	33-312------------------	111000
ORSE	332312---1---1----------	111000
PYCE	1112-1------------------	110111
MOUN	11-2-1------------------	110111
LOIN	-----1------------------	110101
ERLO	----1-------------------	110101
EPAN	--1-1-------------------	110101
LINB	-----1------------------	110101
JUCO	-1-111------------------	110101
LIBO	1-1111------1-----------	110011
GORE	1111-1--1---------------	110010
FRVI	--11-1-1----1-----------	10111
COTR	1-1-11--11----1---------	10101
SAVE	131223--1-11111-1-11----	10100
ARUV	311312--11113-----------	10100
RUID	-----1-1----------------	100111
SABA	-1-123-----221111---1---	011101
SHCA	666666245434442311------	011100
PSME	-11-13-112----1---------	011100
SAGL	34553321233323111212----	011010
SADR	-13-3111111--311--1-----	011001
PIEN	66666655665566444433 11--	011001
SASC	--2----------3----------	011000
HAHY	1----------------1-------	0101
SAFA	1-------------1---1-----	0101
ABLA	552334112312133232331 1-1	0100
SABR	----1---1---1-1---------	0011
EPLA	------------------------1	000111
CARH	----------------1-------	000110
CAMI	--1-----1-111111111112--	000110
SASP	------------------1---1--	000110
DRDR	1-31516666666666666611	00010
SACO	----------11--1---------	000011
CASP	----------1-------------	000010
AGVI	------------1-----------	000010
ORRO	------------1-----------	000010
ANPA	------------1-----------	000010
PIAL	------------1-----------	000010
BOLU	-------1----------------	000001
AGTR	-------1----------------	000001
COMO	-------1112-------------	000000

000000111111111111111111
001111000000000000000011
  00110000000011111111
      0000111100011111
      0111000100100011
       011011   011

STAND CLASSIFICATION

1 Vascular species extracted from TWINSPAN table containing all species.
Time and stand number increases to the left. Stands 1 to 24 refer to transects 1a to 12b (in order)
Species names that correspond to labels are in Appendix 3-3A.
Pseudospecies cut-off levels are 0.0, 0.5, 1.0, 5.0, 10.0 and 25.0.

Table 3-2

TWINSPAN Species-Stand Table for Southeast Lyell Site. Non-vascular Species., 24 Stands.

STAND ORDER

```
                22221211111111 1
                34019236782154807956341 2
```

SPECIES ORDER

HYSP	6644352111--11----------	11110
PTPU	11----------------------	111011
PAAM	-1----------------------	111011
HYPH	-1----------------------	111011
CLRA	11----------------------	111011
CLMU	-1----------------------	111011
CLCO	1-----------------------	111011
CLCE	11----------------------	111011
CLAR	11----------------------	111011
TIAU	11----------------------	111011
PLSC	31---1------------------	111011
MNSP	-1----------------------	111011
AUPA	1-----------------------	111011
BALY	3311-1------------------	111010
DISC	3311-2------------------	111010
DIAC	11---1------------------	111010
CAST	11---1------------------	111010
LOSP	111--1------------------	111000
BASP	111--1------------------	111000
PEAP	111--1------------------	111000
CLGR	-1-1--------------------	111000
PECA	11-1-3------------------	110110
DIFU	2111-2------------------	110110
CLSQ	123333---1--------------	110101
CLSC	--1-11------------------	110101
CLCA	-11111------------------	110101
CEPI	-----1------------------	110101
BARU	--1--1------------------	110101
POEL	--1---------------------	110100
LESP	---1--------------------	110100
CEER	---1--------------------	110100
PYPO	--1---------------------	110100
CAMS	--1---------------------	110100
CLCH	1-3113--11--------------	110011
BUSP	-111-1---------1--------	110011
RHTR	-13-11--11--------------	110011
PTCR	1111-111----------------	11000
PERU	--2-1---1----------1----	10111
HYRE	113313-211---11--1--11--	10110
RISP	---1----1---------------	100111
THSP	--3-1111---1-1-1--------	100110
LERA	----1-------------1-----	10010
DIFL	32343311111111111111--	1000
CAHA	11---1-11---1-----------	011111
CRBL	----1------11-----------	011110
CASI	--1-11-111--111---------	011110
DRUN	3333332132112211111-1--	011011
CACH	111111--111-1-11-1------	011011
TOTO	113122111111111-111-111--	011001
BRGR	2343332332112211112311--	011001
AMSE	111111-1111-1-1-1--1----	011001
GRAP	--1111111111-1-----1-1--	0011
CEPU	1-11111111-2111111-1----	00101
BRCA	113123122233112111111--	00101
TOSP	111111111131321323 21-1--	00100
ACSP	---------------1--------	000110
MAEP	--1---11111111111111-1--	00010
XAEL	-----------111----------	000010
CRWH	-----------11-----------	000010
EUPU	------1----1-1----1-----	000010
BRSA	-------------1----------	000010
POSP	-------1----------------	000001
PAVE	--------1---------------	000001

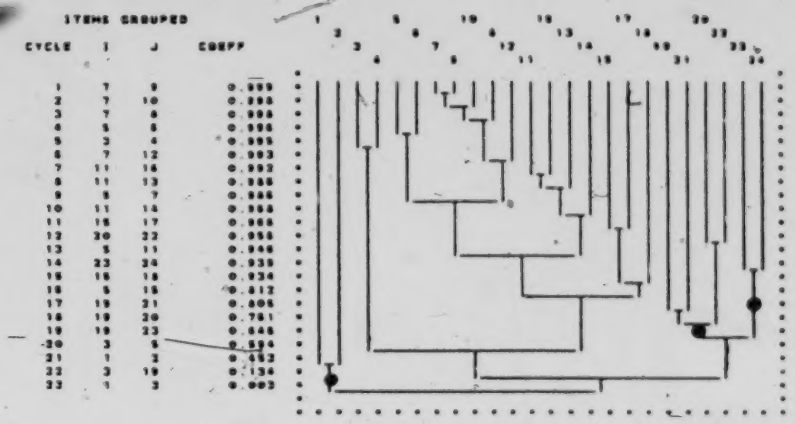
```
000000111111111111111111
001111000000000000000011
  00110000000011111111
     0000111100011111
     0111000100100011
      011011    011

  STAND CLASSIFICATION
```

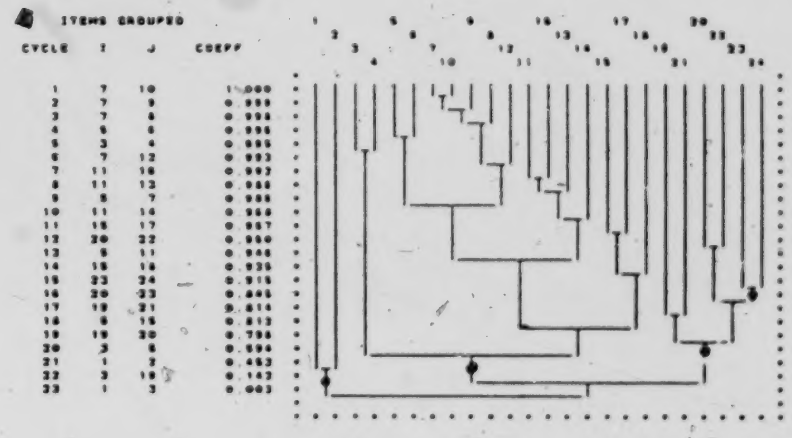
SPECIES CLASSIFICATION

1 Non-vascular species extracted from TWINSPAN table containing all species. Time and stand number increases to the left. Stands 1 to 24 refer to transects 1a to 12b (in order). Species names that correspond to labels are in Appendix 3-4A. Pseudospecies cut-off levels are 0.0, 0.5, 1.0, 5.0, 10.0 and 25.0.

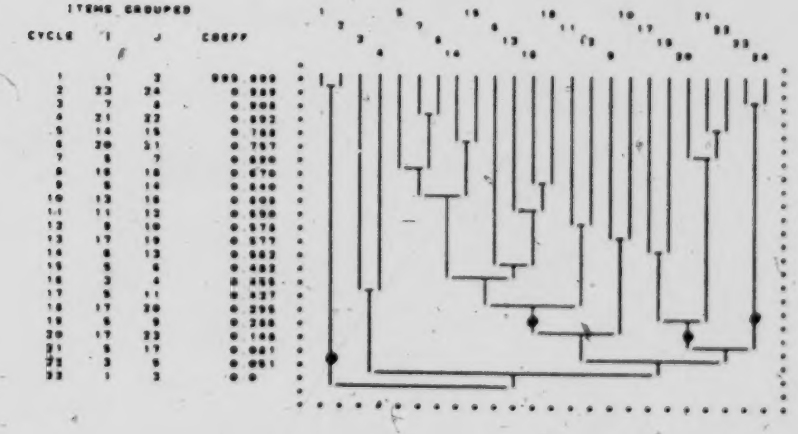
Figure 3-2 CLUSTAN Dendrograms for the Southeast Lyell Glacier Site, Using Raw Data. Unweighted Group Average Clustering Method With Similarity Ratio



(A) All Species



(B) Vascular Species



(C) Non-vascular Species

Items 1-24 refer to transects 1a to 12b (in order)

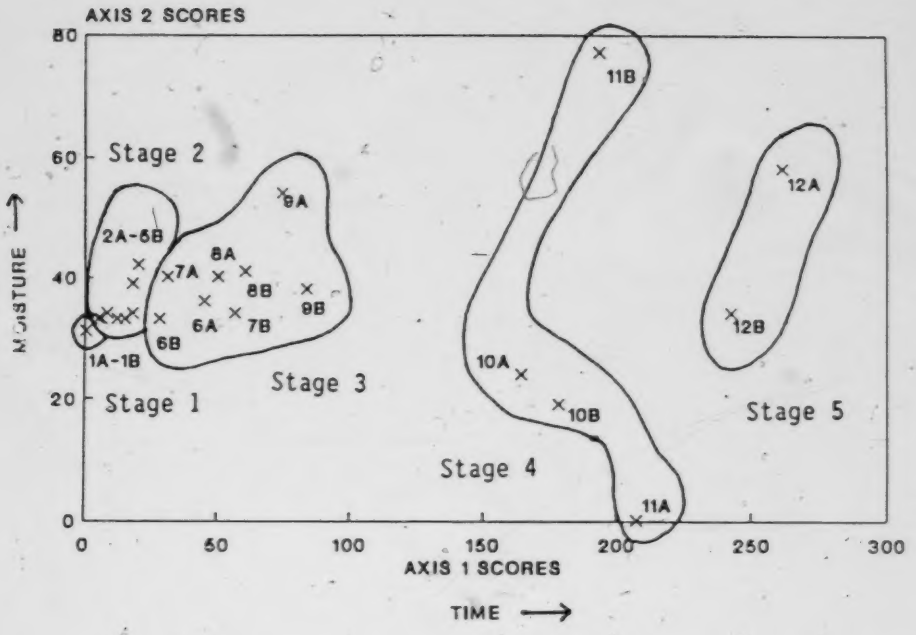


Figure 3-3 DECORANA Ordination of the Southeast Lyell Glacier Site, Based on All Species Using 24 Stands (3 plot Groupings) Percent Variance Explained: Axis 1- 92% Axis 2- 6%

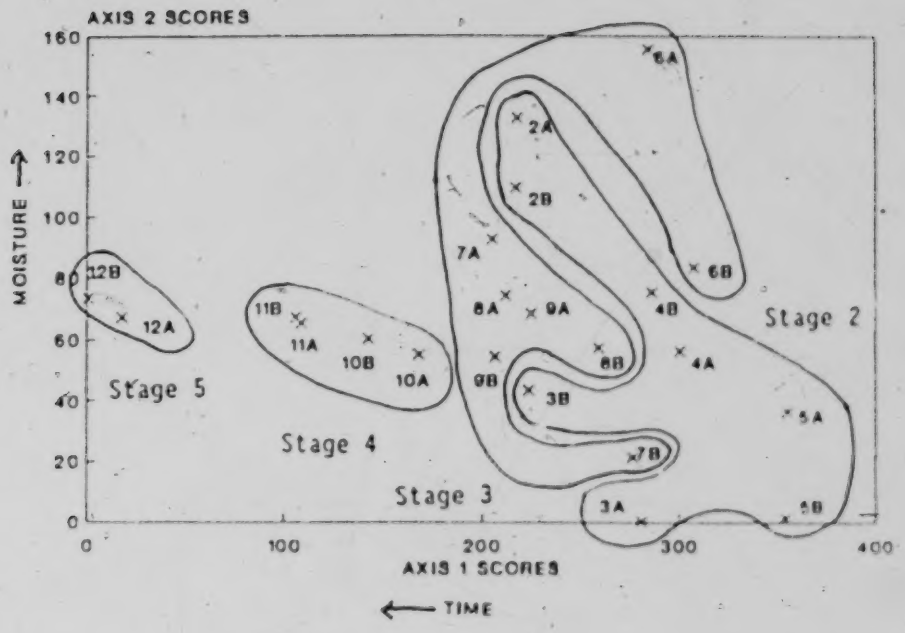


Figure 3-4 DECORANA Ordination of the Southeast Lyell Glacier Site, Based on Non-Vascular Species Using 24 Stands (3 plot Groupings). Percent Variance Explained: Axis 1- 81% Axis 2- 12%. Non-vascular species not present in stands 1A and B

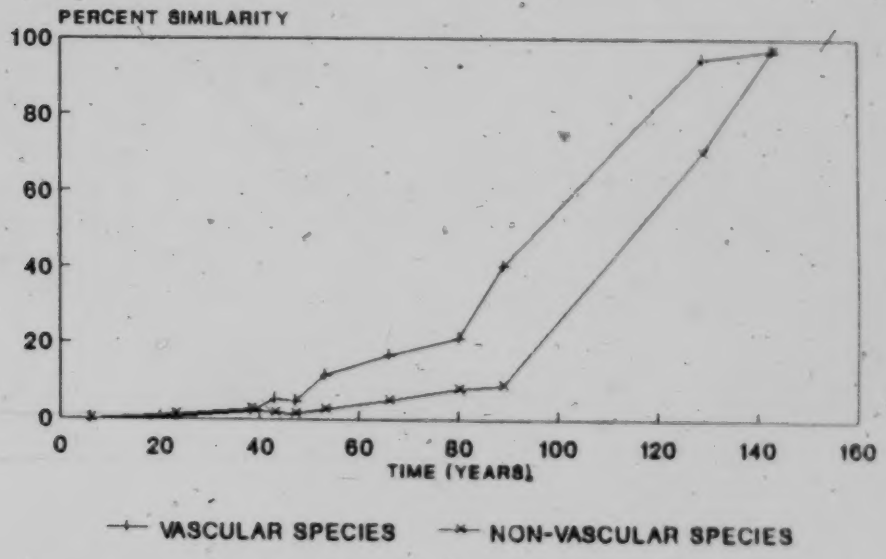
variability. In contrast, substrate moisture (second axis) only explains 6-12 % of the variability (section 3.4.7). With vascular species, variability along the second axis (defined by the spread of points along that axis) increases over time, while with non-vascular species, it decreases.

The rate of change in species composition and abundance, based on similarity to the terminal moraine community stand (Transects 11A and 11B), has two distinct phases (Figure 3-5). On surfaces less than 80 years old, it is moderate. For older stands, the rate of change sharply increases (although this rate of change in the vascular component decreases on Transect 10).

There are some general trends when the species structure curves of the vascular species and non-vascular species are compared (Figures 3-6 and 3-7). In all seral stages, the curves are steeper for the non-vascular species, with more species with intermediate cover (0.1% to 1.0%), as shown by the number in each cover-class. Over time, the slope of the curve increases for both species groups, which indicates an almost consistent increase in richness (Table 3-4, Figure 3-8). Non-vascular total standing crop (combined cover) increases consistently over time (Figure 3-10, Table 3-3) as shown by a shift to the right in the range and actual species positions on the species-structure curves. Vascular total standing crop also increases, but this is due more to increases in a few dominant species rather than a general increase in abundance of many species (Figure 3-9) (i.e., curves do not shift to the right).

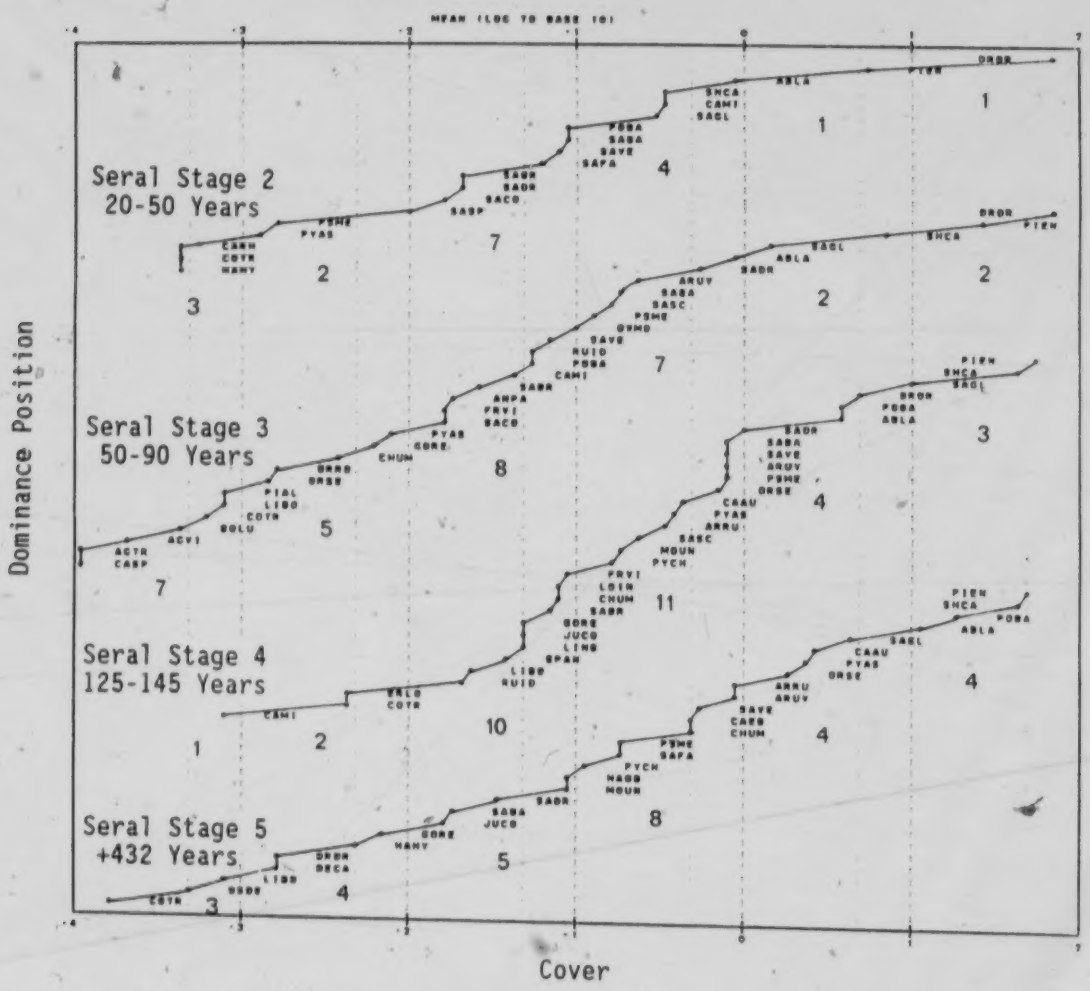
The vascular species structure curve approximates a log-normal distribution in seral stage 4, while in stage 5 it is more geometric (more even distribution of species in all cover classes). The non-vascular species structure curve is also more log-normal for seral stage 4, with geometric distributions for stages 2 and 3.

Figure 3-5 Rate of Change at the Southeast Lyell Glacier Site, Based on All Species Using the Similarity Ratio Coefficient with Transect 11



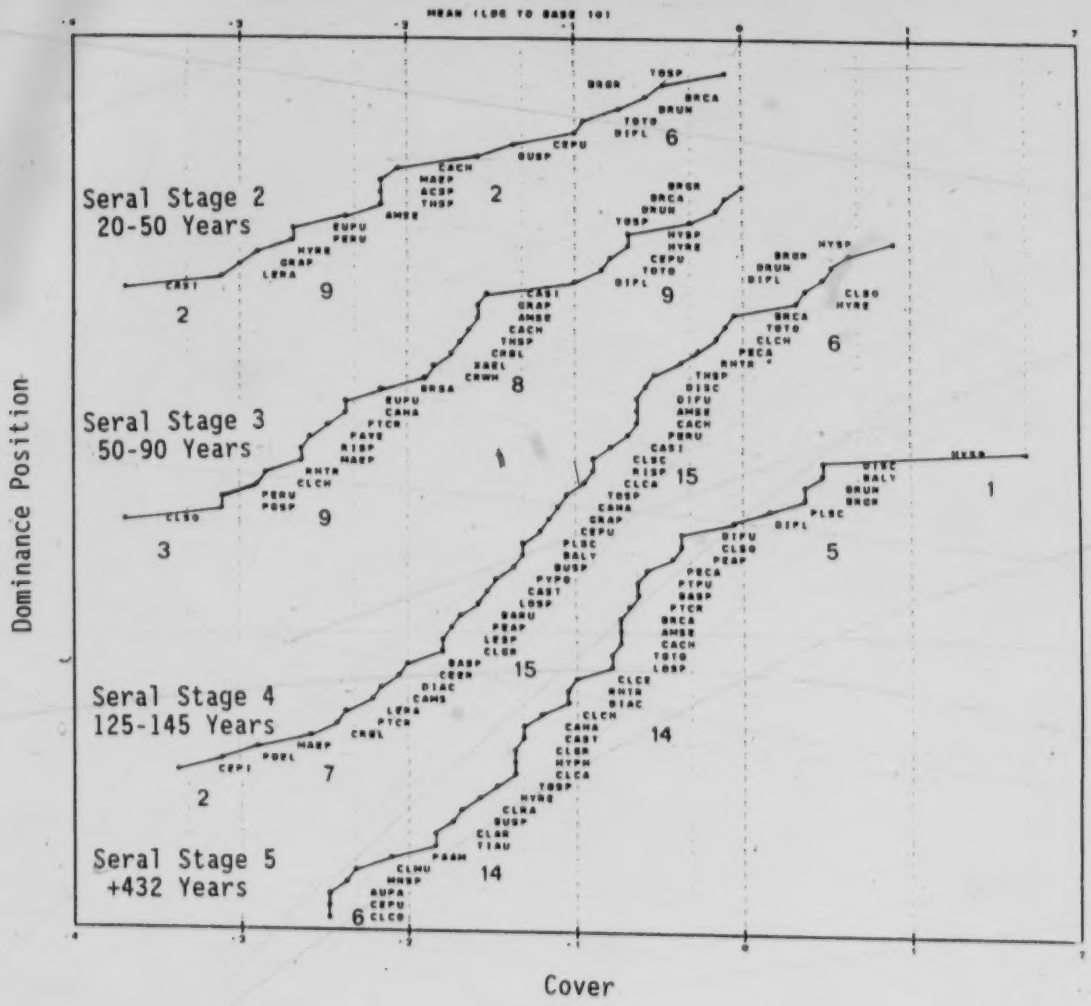
SIMILARITY VALUES ARE BASED ON TERMINAL MORAINE (TRANSECT 11)

FIGURE 3-6 Vascular Species Structure Curves for the Southeast Lyell Glacier Site, for Seral Stages 2 to 5.



Data from stands 1A and 1B not included as there are only three vascular species present (all with less than 1% cover).
The number of species in each cover class is shown under each curve.

Figure 3-7 Non-Vascular Species Structure Curves for the Southeast Lyell Glacier Site, Seral Stages 2 to 5



Stands 1A and 1B do not have any non-vascular species.
The number of species in each cover class is shown under each curve.

TABLE 3-3
CROWN COVER OF MAJOR SPECIES AND PHYSIOGNOMIC GROUPS AT THE SOUTHEAST LYELL SITE
(Averages Based on Five Seral Stages)[1]

Seral Stage Transect Group No. of Plots Surface Age (years)	1 1a, b 6 0-10	2 2a to 5b 24 20-50	3 6a to 9b 24 50-90	4 10a to 11b 12 125-145	5 12a, b 6 432+
Crown Cover (%)					
Tree	< 0.01 (<0.01)	6.3 (1.0)	26.5 (2.6)	65.3 (8.2)	82.1 (14.8)
Shrub (incl. Dryas)	0.3 (0.08)	71.6 (4.4)	77.3 (2.3)	59.1 (6.0)	47.8 (6.0)
Shrub (excl. Dryas)	0.0	0.9 (0.2)	10.0 (1.8)	54.6 (5.4)	47.8 (6.0)
Forb	0.0	0.3 (0.05)	0.2 (0.1)	1.6 (0.4)	4.4 (1.1)
Graminoid	0.0	0.0	< 0.01 < 0.01	0.5 (0.2)	3.2 (0.9)
Moss	0.0	1.9 (0.3)	9.9 (0.3)	24.0 (2.6)	61.5 (8.7)
Lichen	0.0	0.04 (0.02)	0.1 (0.03)	4.3 (0.9)	1.4 (0.3)
Dryas drummondii	0.3 (0.08)	70.7 (4.3)	67.3 (2.1)	4.6 (2.0)	< 0.01 < 0.01
Shepherdia canadensis	0.0	0.3 (0.1)	7.2 (1.6)	40.6 (3.7)	40.5 (5.0)
Abies lasiocarpa	< 0.01 < 0.01	0.9 (0.2)	0.8 (0.4)	3.7 (1.5)	11.5 (2.8)
Picea engelmannii	0.0	5.4 (0.9)	25.5 (2.5)	57.1 (8.0)	51.3 (6.7)
Populus balsamifera	0.0	0.1 (0.04)	0.1 (0.04)	3.7 (1.2)	19.2 (13.4)
Salix glauca var. villosa	0.0	0.3 (0.1)	1.5 (0.6)	9.6 (3.9)	4.3 (1.9)
Hylocomium splendens	0.0	0.0	0.2 (0.1)	7.6 (1.9)	49.7 (7.2)

[1] Standard error of the mean is in brackets.
Values not assumed to be normally distributed.

TABLE 3-4
SOUTHEAST LYELL PLANT COMMUNITY ATTRIBUTE AVERAGES (Based on Five Seral Stages)[1]

Seral Stage	1	2	3	4	5
Transect Group	1a, b	2a to 5b	6a to 9b	10a to 11b	12a, b
No. of Plots	6	24	24	12	6
Surface Age (years)	0-10	20-50	50-90	125-145	432+
All Species					
Richness	1.3	13.3	19.3	38.3	42.0
	(0.2)	(0.6)	(0.8)	(2.3)	(1.6)
Crown Cover (%)	0.3	80.2	107.9	154.9	204.0
	(0.08)	(5.2)	(2.7)	(6.6)	(17.2)
Equitability (C)	0.99	0.78	0.45	0.22	0.18
Diversity (H')	0.02	0.57	1.21	2.20	2.16
Eveness (H'/H max)	0.08	0.17	0.41	0.60	0.57
Vascular Species					
Richness	1.3	5.8	7.4	15.3	14.7
	(0.2)	(0.3)	(0.5)	(1.1)	(0.7)
Crown Cover (%)	0.3	78.3	104.0	126.5	137.5
	(0.08)	(5.1)	(2.6)	(5.7)	(17.9)
Equitability (C)	0.99	0.82	0.48	0.32	0.25
Diversity (H')	0.02	0.43	1.01	1.55	1.68
Eveness (H'/H max)	0.08	0.24	0.51	0.57	0.63
Non-Vascular Species					
Richness	0.0	7.5	12.0	23.0	27.3
		(0.4)	(0.5)	(1.4)	(1.1)
Moss Richness	0.0	6.5	3.8	14.4	16.2
		(0.3)	(0.3)	(0.8)	(0.7)
Lichen Richness	0.0	0.3	1.2	7.0	7.5
		(0.1)	(0.3)	(0.5)	(0.8)
Crown Cover (%)	0.0	1.9	3.9	28.3	66.5
		(0.3)	(0.3)	(3.2)	(6.2)
Equitability (C)	--	0.24	0.16	0.13	0.57
Diversity (H')	--	1.77	2.16	2.44	1.20
Eveness (H'/H max)	--	0.88	0.87	0.78	0.36

[1] Standard error of the mean is in brackets.
Values not assumed to be normally distributed.

Figure 3-8 Trends in Species Richness (Plot Average) at the Southeast Lyell Glacier Site

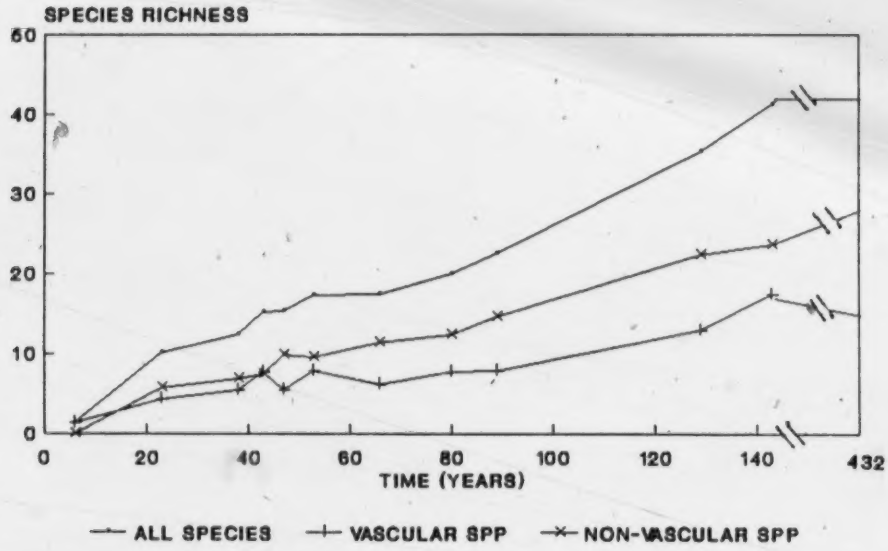


Figure 3-9 Trends in Crown Cover of Major Species at the Southeast Lyell Glacier Site

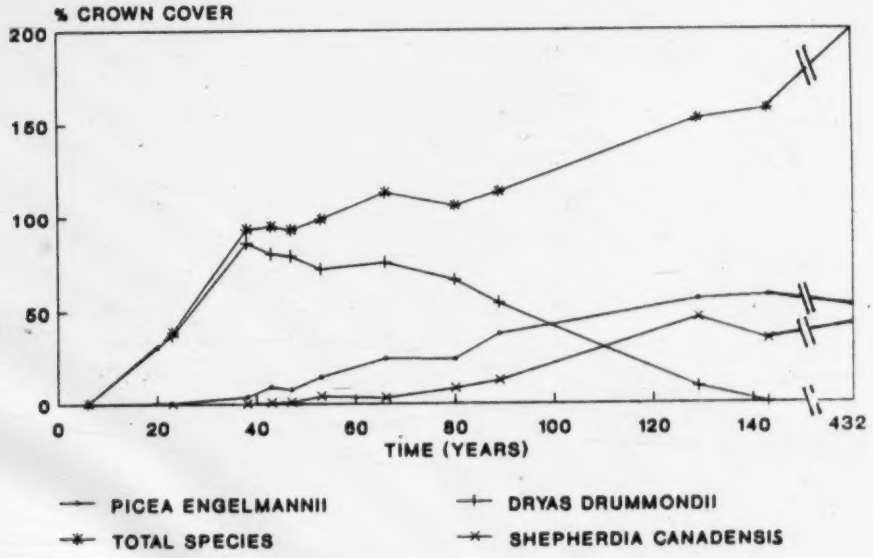
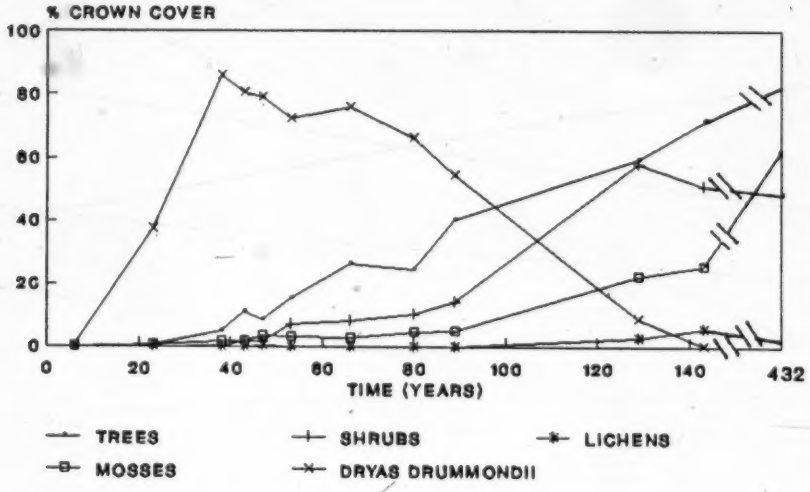


Figure 3-10 Trends in Crown Cover of Growth Form Groups at the Southeast Lyell Glacier Site



The cover-rank of major species helps to clarify the changes in individual species cover over time (similar information is gleaned from the TWINSPAN species-stand table as presented later). There is a larger shift in the most abundant non-vascular species compared to the vascular species. Seven vascular species occupy ranks 1-5 during the succession, while 11 non-vasculars ranked in that position. *Picea engelmannii* and *Shepherdia canadensis* are always ranked within the top four species while *Dryas* declines from 1st in stage 3 to 24th in stage 5. Other late successional species such as *Pyrola asarifolia* increase their ranking over time (16th position and .001% cover in stage 2 to 7th position and 3% cover in stage 5).

Three major species groups can be derived from the TWINSPAN vascular species-stand table (Table 3-1):

1) Species abundant throughout most of the succession
   - *Abies lasiocarpa*, *Dryas drummondii*, *Picea engelmannii*, *Salix glauca* var. *villosa* and *Shepherdia canadensis*

2) Species occurring in low amounts in intermediate-aged seral stages
   - *Oxytropis monticola*, *Salix commutata* and *S. brachycarpa*

3) Species occurring mostly in the older seral stages
   - *Carex aurea*, *C. concinna*, *C. eburnea*, *Chimaphila umbellata*, *Moneses uniflora*, forbs in the family *Orchidaceae*, *Orthilia secunda*, *Populus balsamifera* and *Pyrola* spp.

Four major species groups can be derived from the TWINSPAN non-vascular species-stand table (Table 3-2):

1) Present through most of succession, increasing in older seral stages (though declining in old-growth forest)
   - *Brachythecium groenlandicum*, *Drepanocladus uncinatus* and *Ditrichum flexicaule*

2) Present through most of the succession, declining on older sites
   - *Bryum caespiticium*, *Ceratodon purpureus*, *Ditrichum flexicaule*, *Marasmius epidryas*, *Tortula norvegica*, *T. ruralis*, *Tortella tortuosa*

3) Present only on surfaces older than 100 years
   - *Barbiliphozia lycopodioides*, *Cladonia* spp., *Dicranum scoparium*, *D. fuscescens*, *D. muehlenbeckii* and *Peltigera aphthosa*

4) Present (in low amounts) only in the old growth forest
   - some *Cladonia* spp., *Mnium spinulosum*, *Ptilidium pulcherrimum* and *Timmia austriaca*

Changes in the plant communities along the time gradient are more in terms of species abundance than species composition (especially for vasculars) (see Discussion). Richness increases consistently during the first 140 years (Figure 3-8). Species abundances change gradually over the prisere, both in terms of cover of dominant species and growth-form groups (Figure 3-10 and Table 3-3). The rate of change in plant community attributes is not constant over the time gradient. For example, there is a rather abrupt rate increase in similarity ratio at around 80 years (Figure 3-5).

Dominance concentration (Simpson's C Index) and diversity (H') are mirror images of each other (Figures 3-11 and 3-12). Except for a temporary increase around 50 years, dominance concentration declines constantly for total and vascular species. Decline in dominance concentration for the non-vascular species is very slight, and there is a sharp increase in the old-growth forest. Diversity increases similarly for the three species groupings (Figure 3-12). Although the rate of change of similarity in the communities is most pronounced after 80 years (Figure 3-5), the rate of change in dominance concentration and diversity is actually lower during this time (Figures 3-11 and 3-12). Evenness (H'/H_{max}) of vascular species increases constantly along the chronosequence (Table 3-4, Appendix 3-2). In contrast, non-vascular

Figure 3-11 Trends in Dominance Concentration (C) at the Southeast Lyell Glacier Site

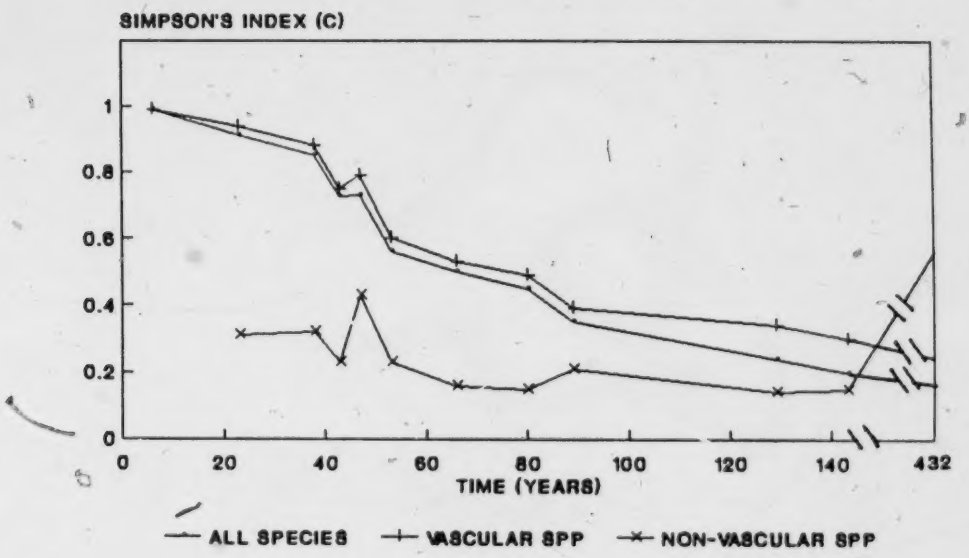
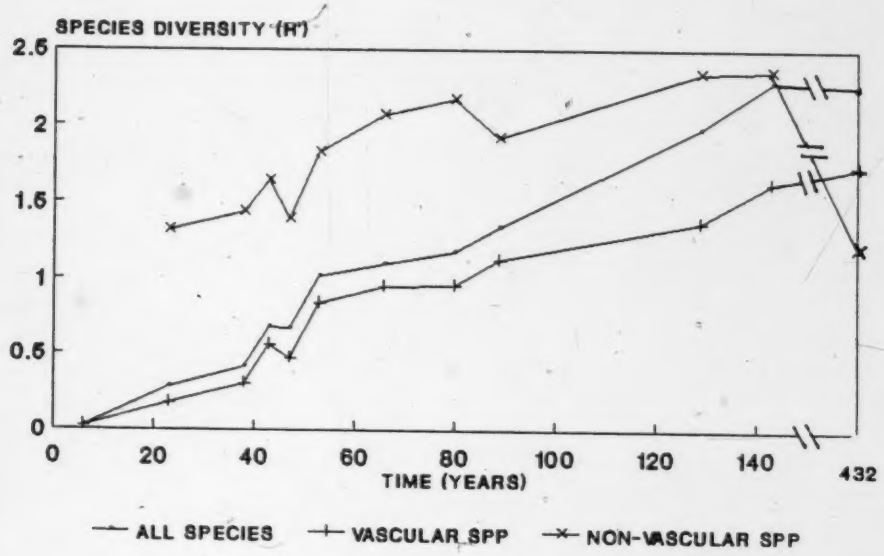


Figure 3-12 Trends in Species Diversity (H') at the Southeast Lyell Glacier Site



species evenness declines slightly over time, with a sharp drop in the old-growth forest.

Notwithstanding the mainly gradual change along the chronosequence, based on the multivariate analysis, the successional sequence can be divided into five seral stages or zones, with the following association names: 1. incipient *Dryas drummondii* 2. *Dryas drummondii* 3. *Picea engelmannii/Dryas drummondii* 4. *Picea engelmannii/Shepherdia canadensis* 5. *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens*. The term "seral stage" is used rather than "community type", "stand" or "vegetation type". "Seral stage" more accurately describes the successional sequence, which is composed of "short" transitory stages. Other terms could be used (e.g., "nodum" from Birks (1980)). Although it is the potential end point (terminal stage) in the succession and not technically a seral stage, the old-growth forest (Stage 5) is given that descriptor, for simplicity.

General descriptions of the five seral stages follow. Detailed information based on these five seral stages is found in Tables 3-3 and 3-4 and in Appendices 3-4A to 3-5B.

Seral Stage 1 Incipient *Dryas drummondii*

Transects 1a-1b Age: 0-10 years Distance from Glacier: 0-50 m

This represents the very early phase of community development. The ground is almost totally bare, with scattered *Dryas drummondii* (0.3% cover) clones up to 10 cm in diameter (although the average is 0.5-3 cm). There are also a few *Abies lasiocarpa* and *Epilobium latifolium* seedlings (Plate 1-5, pg. 64). Non-vascular species are not present at this stage.

Seral Stage 2 *Dryas drummondii*

Transects 2a-5b Age: 20-50 years Distance from Glacier: 50-1300 m

This is the most widespread seral stage, and occurs on the large area deglaciated from the 1930's to the 1950's (see section 1.3.4). It is basically a simple *Dryas drummondii*-dominated community, in which 70.7% of the total 78.3% plant cover is contributed by this one species. Other species occur in much lower amounts: *Picea engelmannii* (5.4%), *Abies lasiocarpa* (0.9%), and *Salix glauca* var. *villosa* (0.3%). Isolated individuals of *Shepherdia canadensis* up to 1.5 m in diameter are present. This, combined with the conifers, gives a "park-like" physiognomy, with 1-2 m tall saplings interspersed among the continuous *Dryas* mat (Plate 1-6, pg. 64). The root parasite *Castilleja miniata* (0.3% cover) is the only common herb. The *Dryas* development on the younger surfaces in this zone is quite variable: just starting in some areas, well developed in others. The onset of senescence in some *Dryas* clones is becoming noticeable on the older portions of this zone.

Non-vascular species are not widespread (total cover 1.9%). They are mostly acrocarpous forms such as *Bryum caespiticium*, *Ceratodon purpureus*, *Ditrichum flexicaule*, *Tortula norvegica* and *T. ruralis*. Smaller amounts of the pleurocarpous mosses *Brachythecium groenlandicum* and *Drepanocladus uncinatus* are present.

There is little influence of slope aspect on this community type as most of the area is covered by gentle to moderately sloping ground moraine interspersed with small De Geer (annual) moraines (Figure 1-8). The trees near the centre of the valley are more stunted, however, probably due to higher winds.

Seral Stage 3 *Picea engelmannii/Dryas drummondii*

Transects 6a-9b Age: 50-90 years Distance from Glacier: 1300-1900 m

At this stage, a multi-stratal community has started to develop (Plate 1-7, pg. 65). Although *Dryas drummondii* is still dominant, with 67% cover, *Picea engelmannii* (25.5%) and *Shepherdia canadensis* (7%) form distinctive low tree and medium shrub strata, respectively. Average *Picea* height ranges from 4 m to 9 m on the 50 and 90 year-old surfaces, respectively (see Appendix 1-2a).

The landscape in this zone is mostly medium (2-3 m tall) moraines separated by abandoned meltwater channels. This is the most heterogeneous stage in the chronosequence due to topographical influence on development. It is characterized by two phases: (1) Open *Dryas* similar to seral stage 2; (2) More closed *Picea* stands, with much less *Dryas*, which is replaced by species such as *Arctostaphylos uva-ursi* which can grow well in the acidic needle litter. Phase 2 occurs mainly along the base of the moraines and in more sheltered hummocky moraine depressions. The largest trees are along the lower moraine slopes, but there are smaller ones on the mid slopes (evidence of subsequent recruitment), and very few on the upper half of the slopes.

Total species richness in stage 3 remains low at 19, although, as Figure 3-6 illustrates, there are several new colonizing species present in low amounts. There is greater diversity and lower dominance concentration compared to stages 1 and 2. Although it is the dominant conifer establishing on the younger surfaces (< 30 years), *Abies lasiocarpa* occurs in this community type in only low amounts (0.8%). *Shepherdia canadensis* is more noticeable in this seral stage, with 7.2% cover and individual crowns up to 2 m wide. A number of *Salix* spp. are present, including *S. glauca* var. *villosa* (1.5%), *S. drummondiana* (0.6%) and *S. barclayi* (0.2%). Herbaceous cover is actually lower than in stage 2 (0.2%) with *Castilleja miniata* again the most common species.

The moss flora is more diverse (represented by 12 species), although there are still no liverworts present. Species are mostly the same as noted for stage 2. Although they occur in slightly higher amounts, overall non-vascular cover remains low (3.9%).

On north- and northeast-facing aspects, pleurocarpous mosses such as *Brachythecium groenlandicum* and *Drepanocladus uncinatus* grow mixed with the *Dryas*. *Hylocomium splendens* forms 0.5 m diameter patches under larger conifers along the lower moraine slopes, and on all aspects where there is adequate shade.

Seral Stage 4 *Picea engelmannii/Shepherdia canadensis*

Transects 10a-11b Age: 125-145 years Distance from Glacier: 1900-2050 m

This seral stage is physiognomically much more developed than stage 3, and constitutes the first mostly closed-canopy forest community type. *Dryas*, with only 4.6% cover, remains only as sporadic patches on the more open knolls (Plate 1-8, pg. 65); *Picea engelmannii* cover is much higher at 57.1%. *Abies lasiocarpa* and *Populus balsamifera* occur in small amounts (both 3.7% cover), usually as saplings or in the sub-canopy. As well, there is the occasional *Pseudotsuga menziesii*. At this stage the forest canopy height ranges from 15 to 23 m.

Well-developed medium and tall shrub strata are present, composed mostly of *Shepherdia canadensis* (40.6%) and *Salix glauca* var. *villosa* (9.6%) (Plate 1-9, pg. 67). Total species richness has also risen sharply to 38 from 19 in seral stage 3. Herbs such as *Carex aurea*, *C. concinna*, *Goodyera repens*, *G. oblongifolia*, *Moneses uniflora* and *Pyrola asarifolia*, which are indicative of a closed forest community, are established in low amounts. Needle litter cover reaches 100% under some trees.

Cover of non-vascular species increases sharply to 28.3% and

includes greater cover of pleurocarpous mosses such as *Hylocomium splendens*, as well as those found in earlier stages. The presence of liverwort species such as *Barbilophozia lycopodioides* and *Lophozia* spp. are indicative of the shadier, more moist substrate conditions at this stage, although their total cover (0.08%) is low. A crust of *Cladonia* squamules and *Ditrichum flexicaule* is common on the drier, more exposed, hummock surfaces.

This stage is not extensive. It encompasses the large moraines just inside the glacial trimline (including the terminal moraine). Although the largest moraines occur in this stage (5-7 m tall), the influence of aspect is less pronounced than in the stage 3, because the canopy cover is mostly continuous. North- and east-facing slopes do have a higher moss cover, however.

Species diversity (*H'*) and evenness (*E*) for all species is much higher than in earlier stages (Figure 3-12, Table 3-4). This community is a mosaic of dense forest with thick *Shepherdia canadensis* understorey and occasional open *Dryas* areas on south-facing slopes. Epiphytic species such as *Hypogymnia physodes* and *Usnea sorediifera* are present on the older trees.

The large terminal moraine has a well-defined outer edge (Plate 1-10, pg 67), and a series of hummocky ridges on the glacier side. No large *Abies* were found on the moraine, although there were a few *Populus balsamifera*. Lower slopes are more open (in contrast to other moraines) and have high *Shepherdia* and *Salix* spp. cover. The moraine crests, on the other hand, have greater tree and moss cover and less shrub cover.

Stage 5 *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens*

Transects 12a and 12b Age: > 432 years

Distance from Glacier: 2050-2200 m

This community is not part of the successional sequence proper (i.e., not a seral stage), but rather represents a potential end point for the primary succession. It is an old-growth forest as shown by the size and age of its trees (Appendix 1-2a) and the numerous decomposing logs on the forest floor (Plate 1-10, pg. 67). There is no sign of disturbance such as fire or flooding. Treefall has resulted in a visually patchy canopy with a heterogeneous understorey with higher shrub and forb cover in the openings and almost 100% bryoid cover in shady areas. This patchy, uneven-aged old-growth forest type is described as "decadent" by some authors (e.g., Day 1972).

There is a more equitable distribution of cover among the tree species: *Picea engelmannii* 51.3%, *Populus balsamifera* 19.1%., and *Abies lasiocarpa* 11.5%. There are also a few scattered *Pseudotsuga menziesii* on more open sites closer to the Glacier River. The upper canopy is 25-30 m high, although younger individuals create a poorly defined sub-canopy. The canopy is composed of different-sized trees with smaller ones (10-16 m tall) infilling the gaps created by treefalls. There is a noticeable increase in conifer size between the terminal moraine slope and adjacent forest outside the trimline (Appendix 1-2A). This climax forest also has a substantial amount of deadwood and a variety of epiphytic species (see Appendix 3-6).

The shrub species have slightly lower cover (47.8%) than in stage 4, but still form a well-defined medium shrub layer dominated again by *Shepherdia canadensis* (40.5%) with lesser amounts of *Salix glauca* var. *villosa* (4.3%) and other *Salix* spp. There are many young *Abies* and *Picea* in the shrub layer, with the former exhibiting layering. It is unusual that this forest community (which has *Pyrola* spp. and orchid species in the forb guild) does not have any *Vaccinium* spp. present (G. La Roi, pers. comm.).

Since *Dryas drummondii* is very rare in this stand, the only common

dwarf shrubs are *Arctostaphylos rubra* and *A. uva-ursi* (both 0.9% cover). The forb and graminoid cover have increased to 4.4% and 3.2%, respectively. The major forbs are orchids - *Habenaria hyperborea*, *H. obtusata*, *Listera borealis* and wintergreens - *Orthilia secunda*, Pyrola asarifolia and *P. chlorantha*, while *Carex aurea*, *C. concinna* and *C. eburnea* are the most common graminoids.

Bryophytes have significantly higher cover ($P < 0.05$) compared to the terminal moraine and are a major component in this community type with 66.5% cover. The feathermoss *Hylocomium splendens* (49.7%) is the dominant species with lesser amounts contributed by *Dicranum scoparium* (3.1%), *Brachythecium groenlandicum* (2.4%), *Drepanocladus uncinatus* (2.4%) and *Pleurozium schreberi* (1.4%). Liverworts form a mixture in the moss carpet with *Barbilophozia lycopodioides* (3.0%) the most common. *Peltigera aphthosa* (0.4%) is the major terrestrial lichen.

The forest floor areas which receive more sunlight have a lower bryophyte cover and more lichens such as *Cladonia* squamules. There is also a higher cover of dwarf shrubs and herbs such as *Arctostaphylos* spp., *Carex eburnea*, *Chimaphila umbellata*, *Geocaulon lividum*, *Orthilia secunda*, *Pyrola chlorantha*, *P. asarifolia*, and juvenile *Populus balsamifera*, *Picea* and *Abies*. The forbs *Habenaria hyperborea* and *Moneses uniflora* which are characteristic of shady, mossy conditions are present in reduced numbers in these more sunny microhabitats .

Dominance concentration (C), calculated for all species, has its lowest value for the whole chronosequence at this site (0.18) (Table 3-4, Figure 3-11). In contrast, diversity (H') and evenness (E) are only slightly lower than their analogues from stage 4 (which are the highest in the chronosequence).

Areas of Seral Stages

The area covered by each seral stage is a function of the glacial

chronology of the site (section 1.3.4) and the rate of succession at each location. An approximation of the proportion of the land area within the glacial trimline (north of the Glacier River) covered by each seral stage is as follows: Stage 1: 5%, Stage 2: 55%, Stage 3: 30%, Stage 4: 10%. The old growth forest, as mapped by McEwen et al. (1982) covers approximately 50 ha, in a wedge-shaped area between the north bank of the Glacier River and the steep south-facing valley slope. Within each seral stage, the morainal "communities" are zonal and have a linear shape where the moraines are separated by abandoned meltwater channels (especially in seral stage 3). In some sites the morainal slopes are irregular, composed of a series of hummocky ridges and depressions. This creates a mosaic of microhabitats, in which conifers and mosses develop first (and attain maximum cover) in the sheltered spots.

Statistical Analysis

In terms of the whole chronosequence, the following community parameters all had a positive correlation with time ($P < .01$): total species (T) richness, vascular species (V) richness, non-vascular species (NV) richness, cover (T,V,NV), diversity (H') (T,V), evenness (E) (T,V). Most of these parameters and indices (except evenness) were also significantly different ($P < .05$) on younger compared to older moraines. Dominance concentration, on the other hand, had a strong negative correlation with time ($P< .01$), for all species, vasculars and non-vascular groups. In terms of growth form, only tree cover and moss cover had a positive ($P <.01$) correlation with time. Tables 3-3 and 3-4 are a summary of these plant community attributes, based on the five seral stages revealed in the TWINSPAN analysis. Appendices 3-2 and 3-3 present this information based on 12 stands (6 plot groupings).

Inter-Morainal Vegetation

The development of vegetation on the inter-morainal areas is distinct from that on adjacent moraines. Near the Southeast Lyell glacier, inter-morainal areas are wet, often with seepages and intermittent streams. These areas often have higher cover of *Salix* spp. than on drier sites, and a distinctly different flora, which indicates wetter conditions (Appendix 3-6).

On surfaces older than 60 years (seral stages 3 and 4), there are some substantial inter-morainal areas. These are mostly abandoned meltwater channels which breach the moraines, and a few are circular to oblong closed depressions. The latter have a finer-textured surface and are more moist (some with standing water) than the well-drained abandoned meltwater channels. These differences in drainage and texture influence the vegetation development.

On the abandoned meltwater channels, the vegetation development is similar to that on the moraines (both structurally and floristically), but does lag behind. Consequently, they are often more open than the vegetation on the adjacent moraines. They are characterized by a continuous *Dryas* cover, along with species which are also present on adjacent moraines including: *Arctostaphylos uva-ursi*, *A. rubra*, *Castilleja miniata*, *Picea engelmannii*, *Salix glauca* var. *villosa* and *Shepherdia canadensis*. In some cases, it includes species (such as *Juniperus communis*, *Potentilla fruticosa*, *Oxytropis monticola*, *Fragaria virginiana* and *Senecio pauperculus*) which are representative of well-drained sub-mesic conditions in the area . The few individuals of *Hedysarum mackenzii* found at the Southeast Lyell site occur in these habitats. *H. mackenzii* is widespread at Mount Robson (Blundon 1989) and it is not known why it is not more abundant at the Southeast Lyell site. Shrub cover is usually moderate (15-25%) and the coniferous trees average 1.5 m tall.

3.4 Discussion

The sequence of plant communities along the time gradient at the Southeast Lyell site does follow a definite course from incipient *Dryas* clones on bare mineral substrates to a mature old-growth forest adjacent to the terminal moraine. In addition to this obvious physiognomic development, there are many, more subtle trends as shown by the results of the data analysis. These are discussed below, using, as a structure, the eight questions which are listed in the introduction to this chapter.

3.4.1 Recognition of Seral Stages

Distinct seral stages can be recognized in the Southeast Lyell prisere. These seral stages are not an artifact of a specific method of analysis, as they were clearly defined in the three multivariate methods used: TWINSPAN, CLUSTAN and DECORANA (Figures 3-1 to 3-4). One reason that these seral stages are so easily defined is because there are only a few dominant species along the chronosequence. In areas where there are many co-dominant species, classification may be more difficult (Heath 1967). At low altitudes, succession proceeds through more seral stages, while at high elevations, the stages are simpler and fewer (Matthews 1978, 1979). This is certainly the case when the Icefield and Southeast Lyell sites are compared.

On both ordination diagrams (Figures 3-3 and 3-4), the separation between seral stages 3 and 4 and seral stages 4 and 5 is more pronounced than separation between the earlier stages (i.e., they are more distinct). As well, the TWINSPAN classification divides the stands in these stages at the lowest level (Figure 3-1). The split between stages 4 and 5 is obviously due to the 300-year gap in surface age. The cause for the separation between stages 3 and 4 is less apparent. It may be associated with the beginning of canopy closure in the 40-year gap between stands 9B and 10A (Tables 1-7 and 3-3) which is reflected in a

change in understorey species. For example, vascular species such as *Carex aurea*, *Moneses uniflora*, *Orthilia secunda* and *Pyrola chlorantha* (Table 3-1) and non-vascular species such as *Cladonia* spp., *Barbilophozia lycopodioides*, *Ditrichum flexicaule*, and *Peltigera canina* first appear (or have greatly increased cover) in seral stage 4.

The old-growth forest at the Southeast Lyell site has been accurately mapped as a *Picea engelmannii-Abies lasiocarpa*/feathermoss vegetation type (C13) in a biophysical inventory of Banff National Park (McEwen et al. 1982). The community description that accompanies this map (Corns and Achuff 1982, p. 85), although not based on field sampling in the immediate vicinity, is quite similar to the actual stand. It includes most of the major species, strong *Abies* regeneration, a sparse herb layer and a well-developed bryoid layer. Major differences are the presence of *Populus balsamifera* and the higher abundance of *Shepherdia canadensis* at the Southeast Lyell site.

The Southeast Lyell old-growth forest community type occurs only in isolated areas (often on old river terraces) of the national parks because it requires a long fire-free period to form (Walker et al. 1982, p. 211). Similar community types occur throughout the Rocky Mountains, from the southern Yukon to southern Alberta (Corns and Achuff 1982, p.85). In the west-central Alberta foothills, Corns (1983) describes a similar type (*Picea glauca/Hylocomium splendens*), although it does not have *Shepherdia canadensis* or *Populus balsamifera* cover. Day (1972) gives a similar description for a "decadent" *Abies-Picea* phase. The Southeast Lyell old-growth stand occurs in an Alberta extension of the *Picea engelmannii-Abies lasiocarpa* forest zone for British Columbia as described by Coupe (1988). *Pseudotsuga menziesii* is not uncommon in stands at lower elevations in this zone. Based on a biogeoclimatic classification for southwestern Alberta, this stand occurs in the northern lower *Picea engelmannii-Abies lasiocarpa* subalpine subzone (Kojima 1980).

Day (1972) and Bray and Struik (1963) suggest that these *Picea-Abies* stands are usually of fire origin and dominated by a succession of *Pinus contorta*, *Picea* and then *Abies*. At the Southeast Lyell site, the *Pinus* phase is missing from the prisere (only one individual was found), although it may have been an early stage in the development of the old-growth forest. Development of the *Abies* component is not strong even after 430 years of stand development. The presence of *Abies* understorey regeneration (layering) may indicate an eventual shift to *Abies* dominance. Veblen (1986), however, suggests that although *Abies* may dominate *Picea* in the understorey, better survivorship of *Picea* means it will remain as the canopy dominant. At the Southeast Lyell site, although in the low shrub stratum *Abies* cover is almost twice as high as *Picea* (2.8% vs. 1.6%), in the tall shrub canopy, it is reversed (2.2% for *Picea*, 0.3% for *Abies*). In the sample plots, there was no *Abies* in the canopy (although tree-sized individuals up to 18 m tall were observed in the stand) but *Picea* cover above 5 m was 43%. Differential growth strategies and survivorship may allow these two ecologically similar species to co-exist. Other *Picea* species such as *P. sitchensis* are also able to persist in the canopy, in competition with other species (e.g., *Tsuga heterophylla*) which may appear to be more suited to the old-growth environment (Alaback 1982). Unlike some authors (e.g., Bloomberg 1950 cf. Day 1972, Rowe 1961), Cormack (1953) believes that the *Picea-Abies* old-growth is an all-aged and self-perpetuating climax vegetation type. This research supports that view for this chronosequence.

The presence of *Populus balsamifera* may be specific to this site, and not a general feature of similar stands in the region, as it is not part of the published *Picea/Abies* community descriptions mentioned above. At the study site, *Populus* is most abundant in a band along the glacial trimline, especially along the north valley slope. This spatial distribution may be related to the location of meltwater streams which may have provided ideal conditions for *Populus* establishment. *Populus* recruitment in the old-growth forest is presently low, with only 0.25%

cover in the shrub strata (< 5 m).

Recognition of seral stages should not mask the actual continuity of developmental processes (Crocker and Major 1955). There is a gradient in species development (Figures 3-9 and 3-10) and, unlike the Glacier Bay site, there are no well-defined breaks in species assemblages (except for the terminal moraine/old-growth forest). Elven (1978) notes it can be difficult to detect distinct vegetation types along these chronosequences because few discontinuities exist in the early development.

Within 20 years, all of the major species in the Southeast Lyell chronosequence, except for *Hylocomium splendens*, are established (although some in very low amounts); this phenomenon is noted from other sites where the climate is relatively warm (e.g., Crocker and Dickson 1957). Zamora (1982) notes that in secondary forest succession in Idaho, 50% of the early seral vegetation is composed of climax species. This proportion between pioneer and climax cover does not occur in the Southeast Lyell prisere until 90 years, due to the overwhelming influence of *Dryas* on the open moraines. On deglaciated terrain, most of the major species which will become established later in the developmental sequence are physiologically able to become established on bare mineral surfaces (Crocker and Major 1955). Of course, many of the understorey humiphytes present in the old-growth forest (e.g., *Carex aurea*, *Habenaria obtusata*, *Hylocomium splendens*, *Moneses uniflora*, *Orthilia secunda* and *Pyrola* spp.) are unlikely to recruit on raw gravel surfaces. Vegetation does not directly develop to these later (coniferous) stages due to different inherent growth rates and the life span of the species and their genetic adaptation to specific physical and chemical environments in the substrate (Crocker and Dickson 1957). In colder environments such as in Norway, there often is a distinct set of early colonizers, including *Dryas* spp. (Elven 1978), which are followed by later species, once the environment is ameliorated.

3.4.2 Diversity of Community Types in the Vegetation

The study of heterogeneity in this prisere can be approached in two ways. (1) The vegetation mosaic of community types present at any one location along the time gradient. (2) Diversity within a particular community type. The first is addressed in this section; the second discussed in the next.

The range of microhabitats (and thus community types) found at the Southeast Lyell site is due to differences in topography (slope, aspect), substrate (moisture conditions, texture) as well as the biotic influence (changes in microhabitat caused by growth of conifers and shrubs). I attempted to minimize the first type of heterogeneity by sampling on similar substrates and topographic positions. This was not always possible, even within a single moraine ridge because sometimes there was great variation in vegetation development (e.g., dense trees at base, open *Dryas* near the moraine crest).

As Figure 3-4 illustrates, there is more non-vascular species heterogeneity between the stands on the intermediate-aged surfaces on seral stage 3 (this is defined as the spread in plot location along the two DECORANA axes). (Heterogeneity in seral stage 2 is high as well, but the position of stands 5A and 5B may be a function of their more open, drier situation on a moderately steep south-facing slope). This community diversity may be due to differential rates of vegetation development on the moraines in this stage (50-90 years), with development of a non-vascular flora in sites with better tree cover. Ordinations based on vascular species (not shown) and total species (Figure 3-3) do not detect this variability because the dominant vascular species do not change (although abundances do). The morainal communities on the older surfaces are less heterogeneous because the moraines at that stage are almost totally tree covered. This may be an example of successional convergence. On younger surfaces, the communities are more uniform because it is on ground moraine, between

small ridges (Plate 1-6, pg. 64).

The contrast between plant community development on the moraines compared to the inter-moraine areas (section 3.3.3) is also greatest on the intermediate-aged surfaces. Vegetation on younger surfaces (40 years old) is more homogeneous, partly due to a more subdued topography, as mentioned above. Abandoned meltwater channels by the terminal moraine are well vegetated with trees and shrubs 4-5 m in height. Unlike the moraine vegetation, *Dryas* cover is still present on these old channels. Conifers are slow to colonize the inter-morainal meltwater channels on the older surfaces. This delay in ecesis may be due to a lack of suitable microhabitats for germination on these open flat surfaces. Also, the high cover of live *Dryas* (almost 100%) may prevent establishment. The latter explanation is more probable.

3.4.3 Diversity Within Stands

Diversity trends in succession are among the most difficult to quantify, since they require accurate data on both species composition and species abundance. Shafi and Yarranton (1973) discuss some of the conceptual and logistical problems associated with monitoring diversity. Odum (1969) postulated that species richness, evenness and stratification all increase during succession, although not always in synchrony. Margalef (1968) and others have attributed maximum species diversity in mature systems to a greater variety of ecological niches. Evidence from some successional studies, however, contradicts this view. For example, increases in organism size, longevity and life cycle complexity can all reduce diversity in mature ecosystems. Species richness may actually decline in mature systems because of a decrease in microhabitat diversity (Perino and Risser 1972).

As noted by Auclair and Geoff (1971) and Shafi and Yarranton (1973) for secondary succession, total species richness and diversity decreased in the Southeast Lyell old-growth forest. This decrease, however, was

only slight (Table 3-4) and appears to be mostly due to increased cover of the feathermoss species *Hylocomium splendens* (Figures 3-8 and 3-12, Table 3-3). In conjunction with this dominance, there was a significant increase ($P < .05$) in dominance concentration and a significant decrease ($P < .05$) in diversity for the non-vascular component. In contrast, vascular diversity is at a maximum in the old-growth forest (Table 3-4), probably due to microsite heterogeneity induced by canopy openings. It may also be partly due to local differentiation of soil properties around individual plants (Mellinger and McNaughton 1975) or finer partitioning of constant density and net productivity among an increasing number of species.

Diversity relationships are often affected by physiognomic, environmental and temporal gradients. For example, diversity increases over time in forests of high environmental stress such as those found on xeric substrates (Auclair and Geoff 1971). This may also be due to ongoing autogenic amelioration at these sites. Ecosystem diversity (i.e., physiognomic complexity, species richness) may be related to the variability of soil properties (Sondheim and Standish 1983) and other substrate characteristics.

Diversity patterns often have two distinct phases: (1) initial rapid increase; (2) a plateau through to mature seral stages. This pattern has been noted in several primary successions on deglaciated terrain (Matthews 1978, Reiners et al. 1971, Sommerville et al. 1982) as well as in old-field secondary successions (Nicholson and Monk 1974). In some secondary forest successions, maximum diversity is quickly reached and then declines over time, as the opportunistic species are replaced with climax species (Zamora 1982). Stable plant species diversity can be maintained over long time periods, even when accompanied by large changes in species composition and physiognomy (Reiners et al. 1971, Perino and Risser 1972). This model is verified with data from the Southeast Lyell site, where there is no significant ($P > 0.05$) change in species richness and diversity (H') between the terminal moraine and

adjacent old-growth forest (over 300 years older).

In discussing diversity trends, the different components should be examined separately. For example, in the Reiners et al. (1971) study, species richness stabilized in the later seral stages, whereas species evenness (*E*) continued to rise slightly, thus creating a slight overall increase in diversity towards maturity. They also conclude that different diversity indices may not be in temporal synchrony. Nicholson and Monk (1974) state, that of the three diversity indices used, species richness stabilized first, followed by information content (*H'*) and then species dominance concentration (*C*). At the Southeast Lyell site, dominance concentration stabilizes first, followed by richness and diversity (*H'*) (Figures 3-8, 3-11 and 3-12). Nicholson and Monk (1974) contend that there might be different mechanisms controlling these indices. For example, they suggest that dominance concentration is regulated by short-term factors (e.g., resource levels) and richness by long-term factors (e.g., community stability). Tilman (1981) says that, due to higher competition stress in nutrient-rich habitats, maximum diversity is found in moderately resource-poor habitats. This resource can be nutrients or space for colonization.

Trends in diversity may also vary for different strata of the same community as reported at Glacier Bay, Alaska (Reiners et al. 1971). This thesis examined only total, vascular and non-vascular diversity, but its data are also amenable to stratal, growth- and life-form diversity analyses.

3.4.4 Rate of Change along Time Gradient

As noted for other sites such as at Mt. Robson (Tisdale et al. 1966), there is a continuous increase or decrease in the abundance of the constituent species (Figure 3-9) and in growth-form groups (Figure 3-10) at the Southeast Lyell site. In gradients where there are no major discontinuities, individual species abundance often approximates a

"normal" or Gaussian distribution (e.g. Mohler 1983). Austin (1981) discusses three models of species response along a gradient: Gaussian response model, ecological displacement model and environmental stress model. The species response in each case may be similar, although the underlying mechanisms differ. At the Southeast Lyell site, the replacement of one species by another is probably due to ecological displacement, caused by autogenic modification of the habitat.

The rate of change does not appear to be constant (Figure 3-5), however. It accelerates after 80 years. The change in rate may be associated with autogenically-induced changes in site conditions. One example is the changes during canopy closure in seral stage 4.

Even if the rate of glacier meltback was constant, the rate of subsequent succession may not be constant (i.e., some stages may be of longer duration, and therefore occupy more area). At the Southeast Lyell site (assuming that this is a chronosequence), development of stages 1 through 3 occurs quickly (within 50 years), while progression through the last 2 stages takes longer. The larger area (approximately 90%) covered by these first three stages are mostly due to the rapid glacial meltback during this century (section 1.3.4).

The rapid development of vegetation after deglaciation is common on mid-latitude sites. Even in Scandinavian sites near the Arctic Circle, Stork (1963) and Worsley and Ward (1974) report colonization by herbs such as *Saxifraga aizoides* one year after deglaciation. On nunataks in Norway, Elven (1980) found no correlation between time of arrival and means of dispersal. Rather, large seed numbers and a short life cycle were the major factors. This is probably true as well at the Southeast Lyell site, especially since the site is relatively small, and borders on mature vegetation.

As with soil development (see section 1.3.7), the <u>overall</u> rate of vegetation development at the Southeast Lyell site seems mostly

controlled by regional climate. In addition, the rate and pattern of pioneer succession on deglaciated terrain is a function of many factors including: valley microclimate, variable snow duration, methods of dispersal, available early colonizers, types of disseminules, and microsite conditions (including availability of fine textured seedbed) (Crocker and Major 1955, Fraser 1967, Bonde 1969, Sigafoos and Hendricks 1969). At the Southeast Lyell Glacier, the major factors appear to be: time since deglaciation, regional climate, altitude, microclimate (aspect is a major influence), substrate characteristics and surface stability. There are other topographic factors which influence the rate of vegetation development (section 3.4.7) such as closeness to the valley wall, moraine size, orientation and spacing.

3.4.5 Non-Vascular And Vascular Plant Development

Development of the vascular and non-vascular vegetation at the Southeast Lyell site is not the same, although there are some similarities. Non-vascular development lags behind vascular species development (illustrated by the rate of change in Figure 3-5). It is only in the old-growth forest that cover of non-vascular species becomes significant (Figure 3-10). The non-vascular species act as a "barometer" of changes in microsite conditions in the understorey. This is especially pronounced during canopy closure, when maximum overstorey-understorey interaction begins (Zamora 1982). There appears to be greater species turnover in the cover-rank (associated with changes in microhabitat) for dominant species in the non-vascular component (compare Figures 3-6 and 3-7).

Multivariate analysis illuminates some of the differences between the two species groups. In the DECORANA ordinations, the stands based on vascular species become more scattered along the second axis on older sites, whereas for the non-vasculars, the reverse is true (Figures 3-3 and 3-4). Along the time gradient, the stand scatter in stand position becomes more pronounced in terms of non-vascular species.

The trends in dominance concentration and diversity (Figures 3-11 and 3-12) are similar for vascular and non-vascular communities, except for the changes to the non-vascular trends caused by the feathermoss development in the oldest stand. The increase in species richness is also quite similar, which may indicate that there is an adequate source of disseminules from adjacent forests.

The moss community accurately reflects the nature of the immediate environment and substratum, because it does not have any conductive tissue (Alpert and Oechel 1982). The changes in moss flora along the succession are due mostly to changes in pH, light and moisture conditions. Mosses such as *Drepanocladus uncinatus* and *Tortula* spp., which occur in the early seral stages at the Southeast Lyell site, are known calciphiles in the European Alps (Geissler 1982). *Barbilophozia* spp. and other liverworts are found only in the old-growth forest because (among other things) they require a more acidic substrate. In proglacial environments at mid-latitudes, small compact cushions and short turf mosses predominate, because of the dry and exposed habitats on recently deglaciated moraines (Longton 1982). At the Southeast Lyell site they include *Bryum caespiticium*, *Ceratodon purpureus*, *Tortella* spp. and *Tortula* spp. The first species is also a major colonizer in similar environments in Norway (Einarsson 1980).

The bryoid flora can be classified into two associations (D. Vitt, pers. comm.). The first is a drier, calcareous substrate association composed of: *Brachythecium groenlandicum*, *Ceratodon purpureus*, *Ditrichum flexicaule*, *Drepanocladus uncinatus*, *Hypnum revolutum*, *Lescuraea radicosa* and *Tortula norvegica*. They occur on the drier, strongly calcareous moraines less than 100-years-old. On the oldest moraines and in the old-growth forest, the association is indicative of more moist, acidic conditions. Species include the mosses *Campylium* spp. and *Hylocomium splendens* and the liverworts *Barbilophozia barbata* and *Lophozia ventricosa*.

It is not as easy to classify the tree species or shrub species into associations since (with the exception of *Populus balsamifera*) they are present throughout most of the succession (Table 3-1). There are two associations in the herb-dwarf shrub guild, however. They are *Dryas drummondii-Castilleja miniata* association on open moraines and *Carex* spp.-*Moneses uniflora*-Orchidaceae-*Pyrola spp.* in the old growth forest.

3.4.6 Uni-Directional Succession

The uni-directionality of succession as described by Odum has been questioned by many ecologists. Drury and Nisbet (1973) cite field evidence to support their contention that patterns of hydrarch and xerarch succession do not follow the classic sequence. Many researchers believe that there is some order to community change but that these trends are not very predictable (Mellinger and McNaughton 1975). In the Southeast Lyell prisere, there is an orderly progression from allogenically-controlled to autogenically-controlled communities. The path of plant community development during succession depends on the following factors: local vegetation, characteristics of the disturbed site (size and intensity of disturbance), stability of initial vegetation, site modification and stochastic elements (Connell and Slatyer 1977, Miles 1979).

The systems approach to ecological succession championed by Odum (1969) and others has limitations, both in the conceptual model and in the nature of field evidence used to test the trends. Salt (1979) and others have criticized Odum's "trends to be expected" as not being emergent properties (i.e., community controlled), but the "collective properties of the individual species". Gorman et al. (1979) questioned the validity of the causal mechanisms which are thought to underlie change in the community function and structure. In their thorough analysis of Odum's hypotheses, Drury and Nisbet (1973) conclude that field studies of succession do not support the expected trends and the

field studies of succession do not support the expected trends and the contention that later stages in succession are consistently unidirectional.

The trends within the trimline are unidirectional (e.g, monotonic changes in the various diversity indices, richness, cover, etc.), perhaps because of the short time period, in which the forest has not fully developed. Perhaps this prisere should be considered as almost two separate entities: (1) the succession within the glacial trimline and (2) the old-growth forest. The juxtaposition of terminal moraine and the old-growth forest communities (Plate 1-10, pg. 67), in which the two are physiognomically similar, but phytosociologically different (Blundon 1989), can lead to erroneous inferences. In 300 years (even assuming a constant climate and no disturbance), the terminal moraine community may look nothing like the present old-growth community. The uncertainty in a time gap of that length should be considered. For example, autogenic mechanisms such as tree-gap dynamics influence the future course of succession at any one location. The time interval within the trimline does, however, conform to Odum's uni-directional model.

3.4.7 Environmental Gradients

The amount of variance explained by the first DECORANA ordination axis (in the transformed matrix) is very high, ranging from 81% based on non-vascular species, to 92% based on total species (Figures 3-3 and 3-4). When the 72 individual plots are ordinated using total species, the first axis still explains 76% of the variability (15% for axis 2). Axis 1 is clearly correlated with time and the associated variations in environmental factors. Elven (1978) also concludes that substrate age is the most important ecological factor governing species distributions. This is verified by ordination results from other research in similar environments (e.g., New Zealand (Sommerville et al. 1982)).

The second axis explains 6-12 % of the variability. Based on

community attributes plotted on the ordination diagram (not shown), the second axis also appears to be a complex-gradient (Whittaker 1975, p. 120) of several factors which appear to be related to moisture. The more moist sites have higher total and vascular cover, higher tree cover (canopy and understorey) and lower shrub cover. The transects were all placed to minimize variability within all factors except time (section 2.2.1). This reduces variability along the other ordination axes, which may partly explain the low variability explained by the second axis. In the sample plots, moisture conditions do not appear to vary enough to have a significant difference on plant community development. When wetter sites within the trimline are examined, the effect of moisture differences becomes important in explaining community development.

Because environmental variables were not measured to develop a chronofunction, the ordination cannot be mapped against a complex-gradient (incorporating soil properties etc.) as defined by Whittaker (1975, p.120). No other factors seem to override the time-complex gradient (re: community development), however.

The Southeast Lyell site has a relatively warm lower subalpine climate, resulting in rapid vegetation development, as compared to the Icefield site (see Section 1.3.6). A thermal microclimatic gradient may exist along the down-valley axis, although it was not detected at the two temperature recording stations (section 1.3.3). Cooler conditions near the present glacier snout may be reflected in a higher proportion of *Abies* seedlings. Based on dendrochronological analysis of *Picea engelmannii* in mature forest adjacent to terminal moraines in eastern B.C., Bray (1965) states that tree growth was often suppressed up to 150 m from glacial termini during periods of glacial maxima, but only suppressed within 5 m of glacial termini during other times. This effect on the growth in adjacent forests would, of course, depend on factors such as size of the glacier. As well, the microclimatic effect of glacial cooling is largely dependant on topography (Bray and Struik 1963). In constricted situations, cold air drainage is concentrated,

whereas on outwash flats, it spreads out and can suppress growth in forests along river terraces. The topography of the Southeast Lyell may be one reason for decreased growth in areas adjacent to the outwash stream, because it would funnel cold-air drainage (as it does katabatic wind) along the valley centre.

For a given surface age, the vegetation nearer the valley centre seems less developed. This is probably due to greater wind exposure. Also, the downvalley sides of the larger moraines are better developed than the upvalley sides, which again relates to exposure. Along transect 10b, for example, the moraines are closer together and trend SE-NW, which gives more shelter from W-E winds. On the same age sites closer to the river, the moraines are smaller and further apart. The major species are much the same along the cross-valley gradient, but species richness is higher on the more sheltered sites near the valley slopes. Species found in these more sheltered sites include *Linnaea borealis*, *Ribes lacustre* and *Rubus idaeus* ssp. *melanolasius*, which are not found elsewhere within the trimline. Their presence may also be partly due to the proximity of seed source from the adjacent subalpine forest. In spite of the above evidence, there was no visual correlation between cross-valley position of stands, and their location on the ordination diagrams (Figures 3-3 and 3-4). This lack of correlation might indicate that only a weak cross-valley gradient exists.

Abies lasiocarpa and *Picea engelmannii* abundance in the low shrub stratum has a bimodal distribution along the chronosequence, with peaks on the 40 year-old surface and the old-growth forest and terminal moraine. This bimodality supports the hypothesis that gap dynamics controls recruitment in the old-growth forest, in which young conifers are establishing to replenish the overstorey (Veblen 1986). *Abies* establishment is greatest in the cool, shady, moist microenvironments under mature *Picea* in the old forest. This reflects a gradient of growing conditions along the chronosequence. *Abies* and *Picea* are both common by the glacier. From transects 2 to 6 (25-55 years) *Abies*

constitutes only 5% of conifer cover (and are all smaller individuals). *Abies* may have initially occurred throughout the chronosequence and then died out on the drier sites. The presence of *Pseudotsuga menziesii* in these drier sites indicates that this may be so, although no dead *Abies* stems were found.

These patterns of tree species may indicate a contemporary environmental gradient down-valley. Although the phenological development of *Dryas* is influenced by aspect, it is in synchrony on similar aspects throughout the chronosequence. Consequently, there may not be enough of a micro-climatic gradient between glacier and terminal moraine to account for the observed tree pattern.

3.4.8 Southeast Lyell Succession Compared with Others

The basic sequence of vegetation development at the Southeast Lyell site is similar to other non-polar sites throughout the world, including New Zealand (Sommerville et al. 1982), Central Europe and Scandinavia (Elven 1980). In general, the similarities are: (1) earliest colonizers are mostly herbs and dwarf shrubs; (2) they are soon replaced by other longer-lived species; (3) diversity increases rapidly at first, but then levels off or declines slightly.

There are some very strong similarities in the major seral stages of primary succession in comparable environments throughout northwestern North America. In the mild, maritime environment at Glacier Bay, Alaska, the prisere proceeds through the following phases: open *Dryas drummondii*, *Alnus crispa* shrub thicket, *Picea sitchensis* forest and finally to *Picea-Tsuga* old-growth forest (Decker 1966). The priseres on the more continental sites at the Kutlan Glacier (Yukon) and Robson Glacier (B.C) are similar to each other. At the Kutlan Glacier site the following phases occur: open *Dryas drummondii*, *Hedysarum mackenzii* herb, *Salix* thicket, *Picea engelmannii* forest (Birks 1980). At the Mount Robson thicket the phases are *Hedysarum mackenzii* herb, open *Dryas*

drummondii and, *Picea engelmannii* forest (Blundon 1989).

The greatest similarities between the Southeast Lyell site and the two preceding seres are (1) the dominance by *Dryas drummondii* early in the succession and (2) the eventual development of a *Picea*-dominated forest. The major differences are (1) the importance of *Shepherdia canadensis*, which requires relatively dry conditions (Watson et al. 1980), and (2) the lack of leguminous nitrogen-fixing species. Although *S. canadensis* does occur at the Kutlan forefield, its strong presence at the Southeast Lyell site probably reflects a warmer climate, due to a more southerly latitude and lower subalpine altitude.

The major physiognomic communities at Glacier Bay in Alaska are characterized by *Dryas*, *Alnus* and *Picea* with the transitions to the last two at around 35 and 100 years, respectively (Crocker and Major 1955). The latter age is similar to the development of closed forest at the Southeast Lyell site, although concurrent changes in understorey vegetation are not as rapid. At the Southeast Lyell site, the major shrubs, *Shepherdia canadensis* and *Salix glauca* var. *villosa*, develop as a strong understorey in the *Picea* communities. Interior Alaska sites have early seral stages which are similar to the Glacier Bay sites, but do not have an *Alnus* phase (Viereck 1970, Scott 1974). As well, the climax communities at these sites are shrub tundra, rather than old-growth forests. Scott (1974) reports a *Dryas octopetala-Shepherdia canadensis* association which is similar to the Southeast Lyell seral stage 2.

In coastal southeast Alaska sites, the *Picea sitchensis-Tsuga* forest may eventually deteriorate into an open *Picea mariana* wetland, due to changes in soil drainage (Lawrence 1958, Reiners et al. 1971). Perhaps due to a more continental climate, there is no evidence of paludification at the Southeast Lyell site. The old-growth forest does not show any evidence of poor or decreasing drainage.

Vegetation development does not appear to be greatly slowed by the

lag in soil development (i.e., regosolic soils under closed canopy forest on the terminal moraine). Climate, along with size of materials is cited as a major factor in ecesis (Heath 1967). In spite of regional differences in climate, the rate of plant succession on glacial forefields is similar at most sites in northwestern North America (Birks 1980). Within about 100 years after deglaciation, coniferous forests, mostly dominated by *Picea*, have developed at Glacier Bay, Alaska (Decker 1966), Mount Robson (Tisdale et al. 1966, Blundon 1989), and Kutlan Glacier, Yukon (Birks 1980) as well as at the Southeast Lyell site. This rate is faster than at some Subarctic sites in central Alaska (e.g., Viereck 1970). In subalpine glacial forefields in Scandinavia, it can take 250-500 years for closed-canopy forest vegetation to develop (Elven 1980).

3.4.9 Ecological Role of Nitrogen-Fixing Species

At the Southeast Lyell site, *Shepherdia canadensis* may have an ecological role similar to that of *Alnus crispa* (Crocker and Major 1955) and *Hedysarum mackenzii* (Blundon 1989) at other sites. These species all have root nodules that can fix atmospheric nitrogen (Gardener and Bond 1957, Lawrence 1958, Tisdale et al. 1966). As well, *Shepherdia* has a growth habit and sociability that traps litter, just like *Alnus*, thus aiding in the buildup of organic matter. Interestingly, at around 100 years at the Southeast Lyell site, the cover of *Shepherdia canadensis* increases just as the cover of *Dryas drummondii* declines (Figure 3-9), perhaps caused by *Shepherdia* shading out the *Dryas*. It does mean, however, that a major N-fixing species is present along the whole chronosequence. This may be a type of "relay floristics" (Egler 1954) in which *Shepherdia canadensis* takes over the ecological role of *Dryas* in the latter part of the succession. Most of the primary successions on deglaciated terrain in North America have at least one other N-fixing species which is prominent after the *Dryas* spp.-dominated phase. These species include: *Alnus crispa* at Glacier Bay, coastal Alaska (Decker 1966); *Hedysarum mackenzii* at Kutlan Glacier, Yukon (Birks 1980) and

Robson Glacier, B.C. (Blundon 1989); *Oxytropis* spp. at Frederika Glacier, interior Alaska (Scott 1974); and *Shepherdia canadensis* at Southeast Lyell, Kutlan and Frederika Glaciers (Birks 1980, Scott 1974). The ecological role played by these species may be similar as suggested by Scott (1974).

As discussed in section 2.4.1, the role of nitrogen-fixing species (especially *Dryas*) in these early successional environments may not be as important as first thought. There were no *Dryas* nodules observed at the Southeast Lyell site. This may be because, although the root crowns of many clones were excavated for age determination, root nodules are most commonly found at depths of at least 20 cm (Wilson 1978). Tisdale et al. (1966), however, state that the abundance of nodules on *Dryas drummondii* and *D. octopetala* at Mt. Robson was only 25% of the abundance of nodules on *Hedysarum mackenzii*.

Alnus, *Dryas* and *Shepherdia* can all grow vigorously at the very low nitrogen levels which characterize fresh glacial debris (Crocker and Major 1955); at the Southeast Lyell site initial N values are almost zero (see Table 1-12). Foliar nitrogen concentrations have been analyzed for *Epilobium latifolium*, *Salix* spp. and *Populus balsamifera* at Kutlan Glacier (Jacobson and Birks 1980) and *Arctostaphylos rubra*, *Picea engelmannii* and *Salix reticulata* at Mt. Robson (Tisdale et al. 1966). In all cases, there were no significant trends from the younger to older moraines. This, along with a lack of visible signs of nitrogen deficiency, suggest that plant growth may not be limited by low soil nitrogen in early stages of succession at these sites, in contrast to Glacier Bay. Experimental work is needed to adequately address this question. For example, in a nutrient-poor environment, the number or size of leaves may be N-limited, rather than the N-concentration of individual leaves (G. La Roi, pers. comm).

3.4.10 Successional Theory

Drury and Nisbet (1973) propose a population-based approach as an alternative to Clements' and Odum's holistic, organismic theory of succession. Their approach emphasizes life history attributes of organisms and uses the consequences of natural selection as the basis for modern succession theory. Successional phenomena are a function of differential growth and survival, and dispersal of species adapted to grow at different points on stress gradients. They suggest that successional theory should be addressed at the organism or physiological level, and not in emergent properties of populations or communities. Pickett (1976, 1982) agrees with this viewpoint and states that the successional sequence can be envisaged as a form of a gradient, along which species are competitively displaced. Analysis of changes in species abundances along the time gradient at the Southeast Lyell site supports this hypothesis. For example, *Dryas drummondii* abundance over time approximates a Gaussian curve (Figure 3-9).

The life history approach has been used by Nobel and Slatyer (1980) and Cattelino et al. (1979) in identifying a minimal number of "vital attributes" of plant species needed to predict successional changes. Connell and Slatyer (1977) use a similar life history approach to present three alternative models (facilitation, tolerance and inhibition) to describe mechanisms of succession. Pickett et al. (1987), expands this to a series of mechanisms of life history processes. The influence of initial floristic composition on succession, first presented by Egler (1954), has been given more recent consideration by Barbour et al. (1980). Using evidence from field studies and published material, Glenn-Lewin (1980) suggests that plant community development over time is more anomalous than predictable.

This thesis research examined changes in plant community composition and structure during succession. There are other ecosystem components that could be examined: community energetics, nutrient cycling and homeostasis (Odum 1969). By analyzing the vascular and non-vascular component together as well as separately, the value of this research is

increased. The results can be used for more comparative work on primary successions in similar environments or as a background to more experimental research.

3.5 Conclusions

1. Including the old-growth forest, there are five discernible seral stages with the following association names: 1. incipient *Dryas drummondii* (0-10 years) 2. *Dryas drummondii* (20-50 years) 3. *Picea engelmannii/Dryas drummondii* (50-90 years) 4. *Picea engelmannii/Shepherdia canadensis* (125-145 years) 5. *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens* (>432 years).

2. The most heterogeneous mosaic of communities occurs on intermediate-aged surfaces. It is a mosaic of two simple community types: (1) open *Dryas* and (2) young conifer thickets.

3. The most diverse community is the old-growth forest, in terms of species richness, evenness and species diversity.

4. Changes in the rate of successional development are demonstrated and viewed as a function of change in environmental gradients related to meso-site and glacial history. Rate of change along the chronosequence is not uniform, but is related to the rate of glacier retreat and intrinsic differences in the response behaviours of participating species.

5. Non-vascular development is slower than (lags behind) vascular development. The non-vascular component may better reflect microsite conditions than the vascular component. Beta diversity in the prisere may be higher for non-vascular species than for vascular species (composition changes more than abundance). There are two major associations in the non-vascular flora which mirror the

microsite changes, from early to late seral stages.

6. Plant community development within the trimline at the Southeast Lyell study site proceeds in a predictable unidirectional sequence. It only takes 140 years for the vegetation to develop from almost bare ground to a closed *Picea*-dominated forest community. The plant community on the terminal moraine is superficially similar to that of the adjacent old-growth forest (in terms of structure and major species), and thus is physiognomically, but not phytosociologically mature (especially in the non-vascular component). There is a shift from allogenically- to autogenically-controlled succession over time.

7. Time is the major variable correlated with stand development (time thus acts as an integrated expression of the variables affecting community development). Other gradients such as moisture and temperature play only a minor part in the succession.

8. The Southeast Lyell prisere is comparable, in terms of general development, as well as some major species, to other primary successions on similar environments throughout the region. There is a nitrogen-fixing species throughout the succession, and *Shepherdia canadensis* may have a similar ecological role as does *Alnus crispa* elsewhere.

9. The old-growth forest appears to be in a dynamic steady state. It is composed of patches of open areas created by treefalls. This adds to community diversity, and allows species with different ecological requirements to co-exist in a mostly closed feathermoss forest.

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4 GENERAL CONCLUSIONS

The Southeast Lyell site provides a well-developed primary vegetation chronosequence, developing from open *Dryas drummondii* communities to closed *Picea engelmannii* forest communities within 143 years. At the Columbia Icefield site, while some of the surfaces have been stable for over 100 years, the community development appears to be restricted to a cyclical succession dominated almost exclusively by *Dryas drummondii*.

Almost all the species which dominate in communities on older moraines at the Southeast Lyell site are present (with low cover) at the Icefield site (*Abies lasiocarpa*, *Picea engelmannii*, *Shepherdia canadensis*, *Salix glauca* var *villosa*). The divergence in pattern and community development is probably due to climatic differences between these two sites, one being in the low subalpine and the other in the high subalpine.

4.1 Nucleation and Facilitation by *Dryas drummondii*

There is some evidence for nucleation by *Dryas drummondii* and that it has a role in quantitative facilitation during succession. Field observations suggest, however, that surface stability (autogenic control) is the major factor in establishment of both *Dryas* and longer-lived woody species. If facilitation is occurring, it is quantitative or non-obligate, in that it enhances community development rather than being required.

4.2 Plant Pattern Development

Dryas drummondii plays a major role in the development of spatial pattern in the vegetation at both study sites. At the Columbia Icefield,

the successional pathway and the dynamics of pattern are cyclical, whereas, at the Southeast Lyell succession proceeds in one direction and is more complex in that more species groups are involved. At the Icefield site, only a *Dryas*-dominated community is present. Early *Dryas* pattern development at both the Sunwapta River and Dome Glacier chronosequences are similar to the Southeast Lyell site, except that there is a cyclical replacement of *Dryas*. *When* clones senesce, they are not replaced by longer-lived woody plants, but rather by *Dryas* seedlings.

The model of pattern development as proposed by Greig-Smith (1964) and modified by Yarranton and Morrison (1974) does appear to predict the observed changes in pattern during primary succession, especially in the simple *Dryas*-dominated systems. For all species groups at both sites, the larger pattern scale generally increases with time while the smaller scale may remain constant. Several scales of pattern are observed which may be related to the morphology of individual plants and to larger scale environmental control. Intensity of pattern is greatest on intermediate-aged surfaces. The sequence of pattern development is repeated for both colonizing *Dryas drummondii* and later persistent species. The number of scales of pattern is greatest on intermediate-aged surfaces, and decline on the older sites.

The trends in pattern development are less clear at the Southeast Lyell site in comparison with the Icefield site. This may be due to greater physiognomic, floristic and microsite complexity in the former. Much of the pattern could be caused by biotic interactions and environmental factors operating at several levels.

Substrate texture and microtopography have a major effect on the establishmnent and growth of Dryas and other species. This influence, while affectting the pattern development, does not override the general clonal growth of Dryas.

4.3 Primary Succession at the Southeast Lyell Site

Including the old-growth forest, there are five discernible seral stages at the Southeast Lyell sere with the following association names: 1. incipient *Dryas drummondii* (0-10 years) 2. *Dryas drummondii* (20-50 years) 3. *Picea engelmannii/Dryas drummondii* (50-90 years) 4. *Picea engelmannii/Shepherdia canadensis* (125-145 years) 5. *Picea engelmannii/Shepherdia canadensis/Hylocomium splendens* (>432 years).

The most heterogeneous mosaic of communities occurs on intermediate-aged surfaces. It is a mosaic of two simple community types: (1) open *Dryas* and (2) young conifer thickets. This heterogeneity is also apparent in the pattern analysis: maximum number of scales recorded for each species group are on intermediate-aged surfaces.

Changes in the rate of successional development at the Southeast Lyell site are demonstrated and viewed as a function of change in environmental gradients related to meso-site and glacial history. Rate of change along the chronosequence is not uniform, but is related to the rate of glacier retreat and intrinsic differences in the response behaviours of participating species.

The development of non-vascular vegetation is slower than that of vascular vegetation and may reflect microsite conditions better than the vascular component. There are two major associations in the non-vascular flora which mirror the microsite changes, from early to late seral stages.

Plant community development within the trimline at the Southeast Lyell study site proceeds in a predictable unidirectional sequence as defined by Odum (1969). The plant community on the terminal moraine is superficially similar to that of the adjacent old-growth forest (in terms of structure and major species), and thus is physiognomically, but not phytosociologically mature (especially in the non-vascular

component). There may be a shift from allogenically to autogenically controlled succession over time.

Time is the major variable correlated with stand development (time thus acts as an integrated expression of the variables affecting community development). Other gradients such as moisture and temperature seem to play only a minor part in determining the course of succession.

The Southeast Lyell primary succession is comparable, in general development and some major species, to other primary successions on similar environments throughout the region. There are nitrogen-fixing species present throughout the time gradient. *Shepherdia canadensis* may have a similar ecological role at this site as does *Alnus crispa* elsewhere.

The old-growth forest appears to be in a dynamic steady state. It is composed of patches of open areas created by treefalls. This increases community diversity, and allows species with different ecological requirements to co-exist in a mostly closed feathermoss forest. Of the communities in the sere, it is the most diverse in species richness, evenness and species diversity.

While the outcome of succession is predictable in a broad sense in that there is the development of a closed-canopy forest at the Southeast Lyell site, putting limits on the actual characteristics is less easy.

4.4 Primary Succession at the Columbia Icefield

Succession on the exposed glacial-fluvial outwash is a cyclical succession of *Dryas drummondii*, as noted for other chronosequences on gravelly substrates in cold and windy climates (Anderson 1967). Unless there is a change in the present climate, this site will probably remain dominated by *Dryas*.

4.5 Importance of this Research

The mechanisms by which the plant communities (especially the Southeast Lyell sere) develop are complicated and cannot be adequately explored using the descriptive approaches employed in this research. This research is important, however, in describing the process of primary succession, thus generating hypotheses for more experimental work, as well as testing hypotheses developed from studies of different seral sequences.

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APPENDIX 1-1A

SOUTHEAST LYELL AND HOHS GLACIERS AERIAL PHOTOGRAPHY COVERAGE [1]

Date	Roll Number	Photo Numbers	Flying Altitude (m)	Focal Length (cm)	Approximate Scale [2]	Emulsion	Index Map
July 1947	A-11100	82-83, 247-250	6,096	15.24	1:30,200	Black and White Panchromatic	82 N "B"
1950	5121x-2428 5122x-2428	87-88 129-130	6,096	15.24	1:30,200	Black and White Panchromatic	
August 1950	A-12765	41-42 84-85	5,182	15.24	1:24,200	Black and White Panchromatic	82 N "A"
September 1955	A-14970	31-33	10,668	15.24	1:60,200	Black and White Panchromatic	82 NW "C"
August 1966	A-19685	115-117	9,144	15.24	1:50,200	Black and White Panchromatic	82 N "C"
August 1972	A-23011 A-23015	159-161 46-47	12,192	15.24	1:70,200	Black and White Panchromatic	82 N "J"
July 1975	A-37213	39-40	10,668	15.24	1:60,200	Colour Infrared	82 N "E"
1977	A-24756	71-72	10,363	15.24	1:58,200	Black and White Panchromatic	82 N "N"

1 All aerial photographs are available at the National Air Photo Library, Ottawa, Ontario.

2 The average altitude of the proglacial moraines is 1490m above sea level. The scale shown is for that altitude.

APPENDIX 1-18

DOME / ATHABSCA GLACIERS AND UPPER SUNWAPTA RIVER AERIAL PHOTOGRAPHY COVERAGE [1]

Date	Roll Number-	Photo Numbers	Flying Altitude (m)	Focal Length (cm)	Approximate Scale [2]	Emulsion	Index Map
July 1938	A-6619	38-48	5,700	15.24	1:25,000	Black and White Panchromatic	83-C/3 "A"
1949	A-12409 160-5206X-1474	4-6	6,096	15.24	1:27,500	Black and White Panchromatic	
1950	160-5205X-2111	110-112	6,096	15.24	1:27,500	Black and White Panchromatic	
1950	160-5204X-2115	56-58	6,096	15.24	1:27,500	Black and White Panchromatic	
September 1951	AS-155	189-191	6,096	15.24	1:27,500	Black and White Panchromatic	83-C/49-1
August 1955	A-14895	24-25 73-74	10,668	15.24	1:57,500	Black and White Panchromatic	83-6 "G"
August 1966	A-19684	27-29 69-72	9,144	15.24	1:47,500	Black and White Panchromatic	83-C "B"
July 1967	A-20145		4,700	15.24	1:18,300	Black and White Panchromatic	83-C "C"
July 1968	A-20888	4-7	4,420	15.24	1:16,400	Black and White Panchromatic	83-C "D"
September 1970	A-21540	169-170 188-190	11,582	15.24	1:63,500		83-C "E"
August 1972	A-23010	193-196	12,192	15.24	1:67,500	Black and White Panchromatic	83-C "J"
August 1972	A-23015	37-40 53-54	12,192	15.24	1:67,500	Black and White Panchromatic	83-C "J"
July 1975	A-37210	104-109	10,668	15.24	1:57,500	Colour Infrared	RS83-C "D"
August 1981	A-25818	7-9 12-14	3,414	15.24	1:9,900	Black and White Panchromatic	

1 All aerial photographs are available at the National Air Photo Library, Ottawa, Ontario

2 The average altitude of the Dome Glacier and Sunwapta River glaciofluvial glaciofluvial outwash is 1910m. The scale shown is for that altitude.

APPENDIX 1-2A

SURFACE AGE DETERMINATION USING GROWTH-RING COUNTS OF WOODY PLANTS ON TRANSECTS ALONG THE SOUTHEAST LYELL GLACIER CHRONOSEQUENCE [1]

Approximate Distance From 1984 Glacier Terminus (m)	Transect Number	Species	[2] Crown Height (m)	Crown Diameter (m)	[3] Plant Age (Years)	[4] Latest Date of Surface Stabilization
20	1a	Dryas drummondii		0.04	3	1981
	1a	Dryas drummondii		0.03	3	1981
25	In front of Youngest Moraine	Abies lasiocarpa	?	?	23	1961
		Abies lasiocarpa	?	?	22	1962
		Picea engelmannii	?	?	21	1963
		Picea engelmannii	?	?	19	1965
		Salix sp.	?	?	16	1968
70	2a	Abies lasiocarpa	0.37	0.4	23	1961
	2a	Abies lasiocarpa	0.27	0.15	22	1962
	2a	Dryas drummondii		2.0	22	1962
	2a	Picea engelmannii	0.31	0.11	21	1963
	2a	Picea engelmannii	0.21	0.21	21	1963
90	2b	Abies lasiocarpa	?	?	20	1964
	2b	Picea engelmannii	?	?	19	1965
	2b	Picea engelmannii	?	?	18	1966
560	3a	Salix sp.	0.65	0.85	34	1950
	3a	Dryas drummondii		0.70	32	1952
	3a	Pseudotsuga menziesii	1.28	1.20	18	1966
1110	4a	Picea engelmannii	2.23	1.14	28	1956
	4a	Picea engelmannii	1.62	1.07	25	1959
	4a	Abies lasiocarpa	0.42	0.33	22	1962
1240	5a	Picea engelmannii	4.5	2.25	39	1945
	5a	Picea engelmannii	2.8	1.60	37	1947
	5a	Populus balsamifera	1.85	1.65	30	1954
	5a	Shepherdia canadensis	1.05	1.40	25	1959
1300	5b	Picea engelmannii	6.0	2.60	45	1939
	5b	Picea engelmannii	5.9	2.75	44	1940
	5b	Salix sp.	?	?	37	1947
	5b	Arctostaphylos uva-ursi		?	25	1959
1480	6a	Picea engelmannii	5.1	2.4	45	1939
	6a	Picea engelmannii	4.8	1.8	42	1942
	6a	Salix glauca var.villosa	0.95	1.45	38	1946
	6a	Abies lasiocarpa	1.35	1.00	36	1948
	6a	Populus balsamifera	2.30	1.20	27	1957
	6a	Shepherdia canadensis	1.20	1.20	27	1957

1 Only the growth-ring counts of the oldest woody plant of each species on each transect is listed here.

2 "?" means no information collected

3 This also corresponds to the minimum time (in years) since the surface became stabilized at that location.

4 This is a conservative estimate of surface age, based on the age of the oldest existing woody plants.

APPENDIX 1-2A

(Cont'd)

Average Distance From Present Glacier Terminus (m)	Transect Number	Species	Crown Height (m)	Crown Diameter (m)	Plant Age (Years)	Latest Date of Surface Stabilization
1610	7a	Picea engelmannii	6.5	2.50	49	1935
	7a	Picea engelmannii	6.5	2.10	48	1936
	7a	Picea engelmannii	6.4	1.50	48	1936
	7a	Picea engelmannii	7.2	3.10	47	1937
1650	7b	Picea engelmannii	6.9	1.45	50	1934
	7b	Picea engelmannii	5.5	1.45	49	1935
	7b	Picea engelmannii	6.6	2.10	43	1941
1700	8a	Picea engelmannii	11.7	2.80	63	1921
	8a	Picea engelmannii	8.3	2.78	61	1923
	8a	Picea engelmannii	7.9	1.80	60	1924
1755	8b	Picea engelmannii	9.0	2.60	63	1921
	8b	Picea engelmannii	10.7	3.20	62	1922
	8b	Picea engelmannii	10.4	2.50	60	1924
1880	9a	Picea engelmannii	8.7	2.65	72	1912
	9a	Picea engelmannii	8.9	2.60	71	1913
	9a	Picea engelmannii	12.3	3.20	70	1914
1890	9b	Picea engelmannii	9.5	2.10	81	1903
	9b	Picea engelmannii	13.2	3.10	80	1904
	9b	Picea engelmannii	9.4	2.60	80	1904
1875	9c	Picea engelmannii	18.4	3.0	101	1883
	9c	Picea engelmannii	18.5	4.5	100	1884
	9c	Picea engelmannii	16.3	2.90	100	1884
1980	10a	Picea engelmannii	25.4	4.0	122	1862
	10a	Picea engelmannii	21.8	3.35	121	1863
	10a	Picea engelmannii	17.2	2.8	118	1866
	10a	Salix scouleriana	9.8	8.0	60	1924
1980	10b	Picea engelmannii	16.5	2.70	111	1873
	10b	Picea engelmannii	17.5	2.65	107	1877
	10b	Picea engelmannii	15.4	2.50	101	1883
2045	11a	Picea engelmannii	21.5	3.55	139	1845
	11a	Picea engelmannii	21.3	2.75	139	1845
Terminal	11a	Picea engelmannii	26.5	3.85	137	1847
Moraine	11a	Picea engelmannii	18.7	2.50	133	1851
	11a	Picea engelmannii	22.2	4.25	132	1852
	11a	Picea engelmannii	24.3	3.20	128	1856
	11a	Populus balsamifera	21.7	7	104	1880
2045	11b	Picea engelmannii	25.0	3.00	131	1853
Terminal	11b	Picea engelmannii	19.8	3.45	130	1854
Moraine	11b	Pseudotsuga menziesii	21.2	5.30	117	1867
2065	12a	Picea engelmannii	33.5	3.50	432	1552
Old Growth	12a	Picea engelmannii	29.6	2.90	413	1571
Forest by	12a	Picea engelmannii	32.2	4.6	398	1586
Terminal	12a	Picea engelmannii	34.0	4.1	380	1604
Moraine	12a	Picea engelmannii	25.2	2.50	376	1608
	12a	Picea engelmannii	23.4	3.80	359	1625

APPENDIX 1-2B

SURFACE AGE DETERMINATION USING GROWTH-RING COUNTS OF WOODY PLANTS ON TRANSECTS ALONG THE DOME GLACIER OUTWASH CHRONOSEQUENCE [1]

Transect	Species	[2] Crown Height (m)	[3] Crown Diameter (m)	[4] Plant Age (years)	Latest Date [5] of Surface Stabilization
Dome-1	Dryas drummondii		1.4	34	1950
Dome-1	Dryas drummondii		1.4	26	1958
Dome-1	Dryas drummondii		1.7	24	1960
Dome-2	Dryas drummondii		2.0	35	1949
Dome-2	Dryas drummondii		carpet	24	1960
Dome-2	Picea engelmannii	0.2	0.2	14	1970
Dome-3	Picea engelmannii	0.2	0.15	36	1948
Dome-3	Dryas drummondii		1.8	34	1950
Dome-4	Shepherdia canadensis	?	?	44	1940
Dome-4	Dryas drummondii		carpet	30	1954
Dome-5	Shepherdia canadensis	0.5	1.5	52	1932
Dome-5	Dryas drummondii		1.5	34	1950
Dome-5	Picea engelmannii	0.25	0.25	25	1959
Dome-6	Shepherdia canadensis	0.45	3.0	55	1929
Dome-6	Picea engelmannii	0.4	0.3	50	1934
Dome-7	Shepherdia canadensis	0.45	1.3	60	1924
Dome-7	Picea engelmannii	0.2	0.25	45	1939
Dome-8	Shepherdia canadensis	0.6	2.3	82	1902
Dome-8	Salix glauca var. villosa	0.5	0.9	73	1911
Dome-8	Salix vestita	0.5	0.7	70	1914
Dome-8	Picea engelmannii	0.35	0.5	41	1943
Dome-8	Arctostaphylos uva-ursi		1.9	34	1950
Dome-9	Salix vestita	0.5	0.8	93	1891
Dome-9	Picea engelmannii	1.2	1.4	74	1910
Dome-9	Shepherdia canadensis	0.6	1.5	72	1912
Dome-9	Arctostaphylos uva-ursi		1.5	28	1956
Dome-10	Shepherdia canadensis	0.4	1.8	104	1880
Dome-10	Shepherdia canadensis	0.5	1.4	100	1884
Dome-10	Salix glauca var. villosa	0.5	2.0	60	1924
Dome-10	Juniperus communis	0.2	1.6	44	1940
Dome-10	Arctostaphylos uva-ursi		2.2	41	1943

1 Only the growth-ring counts of the oldest woody of each species on each transect are listed here.

2 "?" means information not collected.

3 "Carpet" means that Dryas is in a continuous mat, individual clones not distinguishable.

4 This also corresponds to the minimum time (in years) since the surface became stabilized at that location.

5 This is a conservative estimate of surface age, based on the age of the oldest existing woody plants.

APPENDIX 1-2C

SURFACE AGE DETERMINATION USING GROWTH RING COUNTS OF WOODY PLANTS ALONG TRANSECTS ON THE SUNWAPTA RIVER TERRACES [1]

Terrace Surface	Transect	Species	[2] Crown Height (m)	[3] Crown Diameter (m)	[4] Plant Age (years)	Latest Date [5] of Surface Stabilization
"A"	A-1	Dryas drummondii		0.50	12	1972
.5-1m	A-1	Dryas drummondii		0.90	11	1973
above	A-2	Dryas drummondii		2.0	19	1965
active	A-2	Picea engelmannii	0.15	?	18	1966
floodplain	A-3	Dryas drummondii		1.3	22	1962
	A-3	Dryas drummondii		1.5	20	1964
	B-1	Dryas drummondii		2.6	27	1957
	B-1	Salix glauca var. villosa	1.2	2.3	24	1960
	B-1	Salix drummondiana	1.95	1.25	19	1965
	B-2	Dryas drummondii		1.8	30	1954
"B"	B-2	Salix glauca var. villosa	0.7	2.5	23	1961
1.5-1.7m	B-2	Shepherdia canadensis	0.2	0.2	21	1963
above	B-2	Picea engelmannii	1.2	?	20	1964
active	B-3	Dryas drummondii		2.0	30	1954
floodplain	B-3	Salix glauca var. villosa	0.3	0.4	25	1959
	B-3	Picea engelmannii	?	?	22	1962
	B-4	Dryas drummondii		1.8	35	1949
	B-4	Picea engelmannii	0.3	0.35	24	1960
	B-4	Salix glauca var. villosa	1.3	2.6	22	1962
"C"	C-1	Dryas drummondii		2.0	36	1948
2.0-2.3m	C-1	Dryas drummondii		carpet	35	1949
above	C-2	Arctostaphylos uva-ursi		1.4	49	1935
active	C-2	Picea engelmannii	0.38	0.60	24	1960
floodplain	C-2	Salix glauca var. villosa	0.25	1.25	22	1962
"D"	D-1	Picea engelmannii	0.6	1.2	117	1867
2.5m	D-2	Shepherdia canadensis	0.55	0.95	67	1917
above	D-3	Arctostaphylos uva-ursi		3.1	30	1954
active floodplain						

1 Only the growth-ring counts of the oldest woody plants of each species on each transect are listed here.

2 "?" means information not collected

3 "Carpet" means that the Dryas is in a continuous mat, individual clones not distinguishable.

4 This also corresponds to the minimum time (in years) since the surface became stabilized at the location.

5 This is a conservative estimate of surface age, based on the age of the oldest existing woody plants.

APPENDIX 2-1

SOUTHEAST LYELL PATTERN COMPONENT AVERAGES

GROUPED INTO FIVE SURFACE AGES

(Two Smallest-Scale Patterns) [1]

Transect Group No. of Transects	1a, b 2	2a to 5b 8	6a to 9b 8	9c to 11b 5	12a, b 2
Surface Age (years)	0-10	20-50	50-90	105-145	432+
Total Dryas					
Crown Cover (%)	0.3	81.7	86.3	14.3	0.0
Scale 1	1.8	1.7	2.7	2.4	---
Intensity 1	0.4	20.3	25.8	17.2	---
Patch 1	2.1	1.9	4.8	2.3	---
Gap 1	1.5	1.9	1.7	2.3	---
Scale 2	8.1	5.2	7.7	6.6	---
Intensity 2	0.3	19.0	19.8	25.8	---
Patch 2	---	5.3	7.4	2.9	---
Gap 2	---	3.1	2.3	8.4	---
Number of Scales	1.0	4.4	3.4	3.4	0.0
Non-Vascular					
Crown Cover (%)	0.0	2.0	4.0	28.4	66.6
Scale 1	---	2.5	1.7	3.0	9.6
Intensity 1	---	5.4	9.6	27.7	22.6
Patch 1	---	1.1	1.2	1.6	3.9
Gap 1	---	4.3	2.3	4.7	3.0
Scale 2	---	6.7	5.2	10.7	9.0
Intensity 2	---	3.5	5.9	25.6	49.8
Patch 2	---	1.7	3.1	3.6	9.0
Gap 2	---	6.2	6.6	7.5	9.9
Number of Scales	0.0	3.1	4.3	2.6	2.0
Shrub					
Crown Cover (%)	0.0	0.9	6.2	43.0	40.1
Scale 1	---	2.0	2.1	2.7	3.3
Intensity 1	---	9.8	26.7	45.7	41.9
Patch 1	---	---	2.4	2.7	4.5
Gap 1	---	---	3.2	4.0	5.7
Scale 2	---	4.9	5.6	11.1	11.3
Intensity 2	---	6.1	16.8	46.8	47.9
Patch 2	---	---	2.4	3.3	3.9
Gap 2	---	---	7.0	2.7	3.6
Number of Scales	0.0	2.5	4.3	2.8	3.5
Conifer					
Crown Cover (%)	0.0	5.6	23.6	51.4	59.5
Scale 1	---	1.3	2.0	2.2	1.4
Intensity 1	---	21.0	47.2	52.7	38.4
Patch 1	---	0.6	1.7	2.5	2.1
Gap 1	---	1.5	4.1	2.0	1.5
Scale 2	---	4.0	5.6	5.7	3.6
Intensity 2	---	14.2	41.4	46.9	67.0
Patch 2	---	2.1	2.2	4.1	3.3
Gap 2	---	4.5	6.3	2.9	3.9
Number of Scales	0.0	5.0	4.8	4.4	5.0

1 Scale, patch and gap are in metres.
-- Pattern not detected or present.
Dryas drummondii analysis based on total live and dead crown cover.

APPENDIX 2-2

SUNWAPTA RIVER PATTERN ANALYSIS RESULTS

ALL TRANSECTS

(Two Smallest Scale Patterns) [1]

Transect No.	A-1	A-2	A-3	B-1	B-2
Surface Age (years)	12	19	22	27	30
Crown Cover (%)					
Total Dryas	3.5	2.2	3.3	15.3	53.8
Live Dryas	3.5	2.2	3.2	13.5	50.4
Dead Dryas	0	0	0.1	1.8	3.4
Total Dryas					
Scale 1	2.7	2.4	1.2	2.1	1.8
Intensity 1	10.2	8.3	20.6	56.3	51.8
Patch 1	3.0	1.8	1.5	1.8	2.4
Gap 1	3.0	3.3	2.1	2.4	1.5
Scale 2	6.3	7.8	5.7	---	8.7
Intensity 2	6.6	1.6	10.9	---	39.9
Patch 2	3.6	3.0	3.3	---	7.2
Gap 2	10.2	12.9	8.1	---	12.3
Number of Scales	4	4	4	1	3

Transect No.	B-3	B-4	C-1	C-2	D-1
Surface Age (years)	30	35	36	49	117
Crown Cover (%)					
Total Dryas	42.8	71.5	73.9	75.9	78.5
Live Dryas	35.9	61.7	58.7	63.6	66.4
Dead Dryas	6.9	9.8	15.2	12.3	12.1
Total Dryas					
Scale 1	1.8	1.8	1.8	2.1	1.2
Intensity 1	62.7	31.8	35.6	42.1	37.4
Patch 1	1.2	2.1	3.0	3.3	0.9
Gap 1	2.4	1.8	1.5	0.9	1.8
Scale 2	8.1	6.0	4.2	7.8	4.2
Intensity 2	30.8	45.7	25.7	30.9	30.7
Patch 2	8.7	6.3	6.0	10.8	5.7
Gap 2	8.1	6.0	2.4	5.1	2.7
Number of Scales	4	3	4	4	4

1 Scale, patch and gap are in metres.

-- Pattern not detected or present.

Dryas drummondii analysis based on total live and dead crown cover.

APPENDIX 2-3

DOME GLACIER PATTERN ANALYSIS RESULTS

ALL TRANSECTS

(Two Smallest-Scale Patterns) [1]

Transect No. Surface Age (years)	Dome 1 34	Dome 2 35	Dome 3 36	Dome 4 44	Dome 5 52
Crown Cover (%)					
Total Dryas	4.7	54.1	30.1	17.7	75.5
Live Dryas	4.4	50.8	27.6	13.9	49.3
Dead Dryas	0.3	3.3	2.5	3.8	26.2
Total Dryas					
Scale 1	1.5	2.1	2.4	1.2	2.7
Intensity 1	19.5	40.8	37	34.2	33.2
Patch 1	---	2.1	1.8	---	3.9
Gap 1	---	2.4	2.7	---	2.1
Scale 2	5.1	5.1	7.8	3.6	---
Intensity 2	9.6	34.1	36.5	22.1	---
Patch 2	---	5.4	7.5	1.5	---
Gap 2	---	4.8	8.7	5.7	---
Number of Scales	4	4	3	5	1

Transect No. Surface Age (years)	Dome 6 55	Dome 7 60	Dome 8 82	Dome 9 93	Dome 10 107
Crown Cover (%)					
Total Dryas	85.4	79.9	82.6	95.5	88.3
Live Dryas	54.3	50.6	54.8	58.8	41.5
Dead Dryas	31.1	29.3	27.8	36.7	46.8
Total Dryas					
Scale 1	2.4	1.8	1.8	1.5	0.9
Intensity 1	25.7	30.4	30.5	41.5	15.0
Patch 1	3.9	3.3	3	---	1.5
Gap 1	0.9	1.2	0.9	---	0.9
Scale 2	3.9	7.5	8.7	3.6	4.2
Intensity 2	17.4	24	18.3	42.9	11.0
Patch 2	6.0	8.4	---	5.4	5.7
Gap 2	1.8	7.8	---	2.1	2.7
Number of Scales	4	4	3	4	5

1 Scale, patch and gap are in metres.

-- Pattern not detected or present.

Dryas drummondii analysis based on total live and dead crown cover.

APPENDIX 3-1 Similarity Coefficient Matrix of Stands at the Southeast Lyell Site, Based on All Species, 24 Stands (3 Plot Groupings)1

1B	0.453																							
2A	0.004	0.011																						
2B	0.004	0.010	0.995																					
3A	0.002	0.005	0.573	0.616																				
3B	0.002	0.004	0.535	0.576	0.996																			
4A	0.002	0.005	0.597	0.641	0.993	0.985																		
4B	0.002	0.005	0.577	0.620	0.993	0.989	0.999																	
5A	0.002	0.005	0.596	0.640	0.996	0.988	0.999	0.997																
5B	0.002	0.005	0.601	0.645	0.990	0.981	0.999	0.997	0.998															
6A	0.002	0.005	0.641	0.684	0.929	0.913	0.963	0.959	0.955	0.966														
6B	0.002	0.005	0.611	0.655	0.976	0.966	0.994	0.992	0.991	0.985	0.984													
7A	0.002	0.005	0.588	0.630	0.955	0.948	0.982	0.982	0.974	0.982	0.985	0.993												
7B	0.002	0.004	0.516	0.553	0.880	0.883	0.919	0.925	0.906	0.921	0.956	0.944	0.970											
8A	0.002	0.005	0.613	0.650	0.818	0.802	0.872	0.868	0.857	0.879	0.964	0.912	0.936	0.950										
8B	0.002	0.005	0.589	0.630	0.919	0.910	0.954	0.954	0.943	0.957	0.992	0.976	0.987	0.978	0.969									
9A	0.002	0.005	0.529	0.560	0.713	0.703	0.769	0.770	0.752	0.777	0.890	0.817	0.848	0.903	0.966	0.913								
9B	0.002	0.004	0.468	0.495	0.631	0.625	0.696	0.698	0.674	0.701	0.816	0.747	0.799	0.877	0.925	0.845	0.944							
10A	0.000	0.001	0.115	0.120	0.147	0.149	0.178	0.183	0.168	0.185	0.284	0.214	0.237	0.325	0.386	0.315	0.537	0.477						
10B	0.000	0.000	0.012	0.013	0.030	0.035	0.063	0.069	0.051	0.068	0.154	0.098	0.131	0.233	0.260	0.189	0.381	0.417	0.784					
11A	0.000	0.000	0.008	0.008	0.018	0.022	0.044	0.049	0.036	0.049	0.131	0.076	0.098	0.183	0.223	0.153	0.337	0.342	0.805	0.796				
11B	0.000	0.000	0.004	0.005	0.019	0.024	0.054	0.060	0.040	0.058	0.141	0.086	0.124	0.224	0.251	0.177	0.364	0.428	0.720	0.956	0.744			
12A	0.000	0.000	0.003	0.003	0.013	0.016	0.035	0.040	0.027	0.038	0.097	0.057	0.080	0.145	0.166	0.122	0.248	0.256	0.543	0.643	0.604	0.681		
12B	0.000	0.000	0.003	0.003	0.013	0.017	0.037	0.042	0.029	0.041	0.105	0.062	0.087	0.157	0.180	0.131	0.269	0.279	0.591	0.719	0.655	0.732	0.939	

1 Calculated from the similarity ratio (see text), using all species with raw data.

APPENDIX 3-2

SOUTHEAST LYELL PLANT COMMUNITY ATTRIBUTE AVERAGES

(Based on Six Plot Groupings)

Transect Group [1]	1a, b	2a, b	3a, b	4a, b	5a, b	6a, b
Surface Age (years)	6	23	38	43	47	53
All Species						
Richness	1.3	10.2	12.3	15.2	15.3	17.3
Crown Cover (%)	0.3	39.3	93.4	95.0	93.1	98.8
Equitability (C)	0.99	0.91	0.85	0.73	0.73	0.56
Diversity (H')	0.02	0.28	0.41	0.68	0.67	1.02
Eveness (H'/H max)	0.07	0.12	0.16	0.25	0.25	0.36
Vascular Species						
Richness	1.3	4.3	5.5	7.7	5.5	7.8
Crown Cover (%)	0.3	38.6	91.8	93.3	89.4	95.4
Equitability (C)	0.99	0.94	0.88	0.75	0.79	0.60
Diversity (H')	0.02	0.18	0.30	0.56	0.47	0.84
Eveness (H'/H max)	0.07	0.12	0.18	0.27	0.28	0.41
Non-Vascular Species						
Richness	0.0	5.8	6.8	7.5	9.8	9.5
Moss Richness	0.0	5.7	5.7	6.3	8.2	8.2
Lichen Richness	0.0	0.0	0.2	0.2	0.7	0.5
Crown Cover (%)	0.0	0.7	1.6	1.7	3.7	3.4
Equitability (C)	--	0.31	0.32	0.23	0.43	0.23
Diversity (H')	--	1.32	1.44	1.64	1.39	1.83
Eveness (H'/H max)	--	0.75	0.76	0.81	0.61	0.81

1 Each transect group contains 6 community analysis plots, 3 per transect.

APPENDIX 3-2

(Cont'd)

Transect Group [1]	7a, b	8a, b	9a, b	10a, b	11a, b	12a, b
Surface Age (years)	66	80	89	129	143	432
All Species						
Richness	17.5	20.0	22.5	35.3	41.2	42.0
Crown Cover (%)	113.3	106.0	113.7	152.2	157.5	204.0
Equitability (C)	0.50	0.45	0.35	0.24	0.20	0.18
Diversity (H')	1.10	1.18	1.34	1.98	2.28	2.16
Eveness (H'/H max)	0.38	0.39	0.43	0.56	0.61	0.58
Vascular Species						
Richness	6.2	7.7	7.8	13.0	17.5	14.7
Crown Cover (%)	110.4	101.4	108.8	126.9	126.2	137.5
Equitability (C)	0.53	0.49	0.39	0.34	0.30	0.25
Diversity (H')	0.95	0.96	1.13	1.37	1.63	1.68
Eveness (H'/H max)	0.52	0.47	0.55	0.53	0.57	0.63
Non-Vascular Species						
Richness	11.3	12.3	14.7	22.3	23.7	27.3
Moss Richness	10.0	10.5	11.0	14.3	14.5	16.2
Lichen Richness	0.7	1.2	2.7	6.5	7.5	7.5
Crown Cover (%)	2.9	4.6	4.8	25.3	31.3	66.5
Equitability (C)	0.16	0.15	0.21	0.14	0.15	0.57
Diversity (H')	2.07	2.17	1.92	2.34	2.36	1.20
Eveness (H'/H max)	0.85	0.86	0.72	0.75	0.75	0.36

1 Each transect group contains 6 community analysis plots, 3 per transect.

APPENDIX 3-3

CROWN COVER OF MAJOR SPECIES AND PHYSIOGNOMIC GROUPS AT THE SOUTHEAST LYELL SITE

(Based on Six Plot Groupings)

Transect Group [1]	1a, b	2a, b	3a, b	4a, b	5a, b	6a, b
Surface Age (years)	6	23	38	43	47	53
Crown Cover (%)						
Tree	< 0.01	0.8	5.1	10.9	8.6	15.4
Shrub (incl. *Dryas*)	0.3	37.4	86.4	82.0	80.7	79.5
Shrub (excl. *Dryas*)	0.0	0.0	0.4	1.6	1.6	7.1
Forb	< 0.01	0.4	0.3	0.4	0.2	0.5
Graminoid	0.0	0.0	0.0	0.0	0.0	< .01
Moss	0.0	0.7	1.6	1.7	3.5	3.3
Lichen	0.0	0.0	0.01	< 0.01	0.1	0.1
Dryas drummondii	0.3	37.4	86.0	80.4	79.1	72.4
Shepherdia canadensis	0.0	0.0	0.0	0.6	0.8	4.2
Abies lasiocarpa	< 0.01	0.4	1.1	1.5	0.6	0.6
Picea engelmannii	0.0	0.4	3.9	9.3	7.8	14.8
Populus balsamifera	0.0	0.0	0.04	0.1	0.2	0.01

Transect Group [1]	7a, b	8a, b	9a, b	10a, b	11a, b	12a, b
Surface Age (years)	66	80	89	129	143	432
Crown Cover (%)						
Tree	26.2	24.4	40.1	59.3	71.3	82.1
Shrub (incl. *Dryas*)	84.1	76.8	68.7	67.0	51.3	47.8
Shrub (excl. *Dryas*)	8.2	10.4	14.3	58.1	51.1	47.8
Forb	0.03	0.2	0.1	0.6	2.7	4.4
Graminoid	0.0	< 0.1	0.0	0.1	0.9	3.2
Moss	2.9	4.5	4.8	22.3	25.6	61.5
Lichen	0.04	0.1	0.1	3.0	5.6	1.4
Dryas drummondii	75.9	66.4	54.4	6.9	0.2	< 0.01
Shepherdia canadensis	3.3	8.4	12.8	46.6	34.6	40.5
Abies lasiocarpa	1.3	< 0.1	1.5	1.2	6.1	11.5
Picea engelmannii	24.8	24.3	38.1	56.3	58.0	51.3
Populus balsamifera	0.1	0.0	0.1	1.6	5.9	19.2

1 Each Transect group contains 6 community analysis plots, 3 per transect.

APPENDIX 3-4A
STATISTICAL SUMMARY FOR VASCULAR SPECIES FROM SEADYN ANALYSIS, SERAL STAGE 1, SOUTHEAST LYELL SITE

		SERAL STAGE 1 0-10 YEARS TRANSECTS 14 & 15		
SPECIES NAME	VARIABLE	FREQ %	MEAN	STD ERR
Abies lasiocarpa	ABLA	17	0.0003	0.0003
Pinus albicaulis	PIAL	0	0.0	0.0
Picea engelmannii	PIEN	0	0.0	0.0
Populus balsamifera	POBA	0	0.0	0.0
Pseudotsuga menziesii	PSME	0	0.0	0.0
Arctostaphylos rubra	ARRU	0	0.0	0.0
Arctostaphylos uva-ursi	ARUV	0	0.0	0.0
Chimaphila umbellata ssp. occidentalis	CHUM	0	0.0	0.0
Dryas drummondii	DRDR	100	0.26	0.08
Juniperus communis	JUCO	0	0.0	0.0
Linnaea borealis ssp. americana	LINB	0	0.0	0.0
Rubus idaeus ssp. melanolasius	RUID	0	0.0	0.0
Salix barclayi	SABA	0	0.0	0.0
Salix brachycarpa ssp. brachycarpa	SABR	0	0.0	0.0
Salix commutata	SACO	0	0.0	0.0
Salix drummondiana	SADR	0	0.0	0.0
Salix farriae	SAFA	0	0.0	0.0
Salix glauca var. villosa	SAGL	0	0.0	0.0
Salix scouleriana	SASC	0	0.0	0.0
Salix sp.	SASP	0	0.0	0.0
Salix vestita	SAVE	0	0.0	0.0
Shepherdia canadensis	SHCA	0	0.0	0.0
Anemone parviflora	ANPA	0	0.0	0.0
Castilleja miniata	CAMI	0	0.0	0.0
Castilleja rhexifolia	CARH	0	0.0	0.0
Corallorhiza trifida	COTR	0	0.0	0.0
Epilobium angustifolium	EPAN	0	0.0	0.0
Epilobium latifolium ssp. latifolium	EPLA	17	0.0005	0.0005
Erigeron lonchophyllus	ERLO	0	0.0	0.0
Fragaria virginiana ssp. glauca	FRVI	0	0.0	0.0
Goodyera repens var. repens & G. oblongifolia	GORE	0	0.0	0.0
Habenaria obtusata	HAOB	0	0.0	0.0
Habenaria hyperborea	HAHY	0	0.0	0.0
Listera borealis	LIBO	0	0.0	0.0
Moneses uniflora	MOUN	0	0.0	0.0
Orchis rotundifolia	ORRO	0	0.0	0.0
Orthilia secunda	ORSE	0	0.0	0.0
Osmorhiza depauperata	OSDE	0	0.0	0.0
Oxytropis monticola ssp. monticola	OXMO	0	0.0	0.0
Pyrola asarifolia	PYAS	0	0.0	0.0
Pyrola chlorantha	PYCH	0	0.0	0.0
Agropyron trachycaulum var. trachycaulum	AGTR	0	0.0	0.0
Agropyron violaceum	AGVI	0	0.0	0.0
Carex aurea and C. concinna	CAAU	0	0.0	0.0
Carex eburnea	CAEB	0	0.0	0.0
Carex sp.	CASP	0	0.0	0.0
Deschampsia cespitosa ssp. cespitosa	DECA	0	0.0	0.0
Botrychium lunaria	BOLU	0	0.0	0.0
Lonicera involucrata	LOIN	0	0.0	0.0
Number of Plots (n)			6	
Species Richness			3	
Total Crown Cover (%)			0.26	
Dominance Concentration (C)			0.99	
Diversity (H') (natural logs)			0.02	

APPENDIX 3-4B
STATISTICAL SUMMARY FOR VASCULAR SPECIES FROM SEADYN ANALYSIS,
SERAL STAGES 2 AND 3, SOUTHEAST LYELL SITE

		SERAL STAGE 2 20-50 YEARS TRANSECTS 2A TO 5B			SERAL STAGE 3 50-90 YEARS TRANSECTS 6A TO 9B		
SPECIES NAME	VARIABLE	FREQ %	MEAN	STD ERR	FREQ %	MEAN	STD ERR
Abies lasiocarpa	ABLA	88	0.89	0.16	54	0.84	0.36
Pinus albicaulis	PIAL	0	0.0	0.0	4	0.0008	0.0008
Picea engelmannii	PIEN	100	5.35	0.91	100	25.50	2.45
Populus balsamifera	POBA	21	0.08	0.05	13	0.05	0.04
Pseudotsuga menziesii	PSME	4	0.002	0.002	13	0.13	0.10
Arctostaphylos rubra	ARRU	0	0.0	0.0	0	0.0	0.0
Arctostaphylos uva-ursi	ARUV	0	0.0	0.0	29	0.23	0.16
Chimaphila umbellata ssp. occidentalis	CHUM	0	0.0	0.0	4	0.004	0.004
Dryas drummondii	DRDR	100	70.70	4.26	100	87.26	2.14
Juniperus communis	JUCO	0	0.0	0.0	0	0.0	0.0
Linnaea borealis ssp. americana	LINB	0	0.0	0.0	0	0.0	0.0
Rubus idaeus ssp. melanolasius	RUID	0	0.0	0.0	4	0.05	0.05
Salix barclayi	SABA	21	0.08	0.06	21	0.19	0.10
Salix brachycarpa ssp. brachycarpa	SABR	8	0.02	0.02	8	0.03	0.02
Salix commutata	SACO	4	0.02	0.02	8	0.02	0.01
Salix drummondiana	SADR	13	0.02	0.02	33	0.57	0.38
Salix farriae	SAFA	8	0.06	0.06	0	0.0	0.0
Salix glauca var. villosa	SAGL	38	0.29	0.13	100	1.53	0.46
Salix scouleriana	SASC	0	0.0	0.0	8	0.16	0.15
Salix sp.	SASP	8	0.01	0.008	0	0.0	0.0
Salix vestita	SAVE	21	0.08	0.05	21	0.07	0.04
Shepherdia canadensis	SHCA	29	0.34	0.12	83	7.17	1.65
Anemone parviflora	ANPA	0	0.0	0.0	4	0.02	0.02
Castilleja miniata	CAMI	96	0.32	0.05	38	0.04	0.02
Castilleja rhexifolia	CARH	4	0.0004	0.0004	0	0.0	0.0
Corallorhiza trifida	COTR	4	0.0004	0.0004	8	0.0006	0.0005
Epilobium angustifolium	EPAN	0	0.0	0.0	0	0.0	0.0
Epilobium latifolium ssp. latifolium	EPLA	0	0.0	0.0	0	0.0	0.0
Erigeron lonchophyllus	ERLO	0	0.0	0.0	0	0.0	0.0
Fragaria virginiana ssp. glauca	FRVI	0	0.0	0.0	8	0.02	0.01
Goodyera repens var. repens & G. oblongifolia	GORE	0	0.0	0.0	4	0.006	0.006
Habenaria obtusata	HAOB	0	0.0	0.0	0	0.0	0.0
Habenaria hyperborea	HAHY	4	0.0004	0.0004	0	0.0	0.0
Listera borealis	LIBO	0	0.0	0.0	4	0.0008	0.0008
Moneses uniflora	MOUN	0	0.0	0.0	0	0.0	0.0
Orchis rotundifolia	ORRO	0	0.0	0.0	4	0.002	0.002
Orthilia secunda	ORSE	0	0.0	0.0	8	0.001	0.001
Osmorhiza depauperata	OSDE	0	0.0	0.0	0	0.0	0.0
Oxytropis monticola ssp. monticola	OXMO	0	0.0	0.0	21	0.10	0.09
Pyrola asarifolia	PYAS	4	0.001	0.001	17	0.01	0.005
Pyrola chlorantha	PYCH	0	0.0	0.0	0	0.0	0.0
Agropyron trachycaulum var. trachycaulum	AGTR	0	0.0	0.0	4	0.00008	0.00008
Agropyron violaceum	AGVI	0	0.0	0.0	4	0.0002	0.0002
Carex aurea and C. concinna	CAAU	0	0.0	0.0	0	0.0	0.0
Carex eburnea	CAEB	0	0.0	0.0	0	0.0	0.0
Carex sp.	CASP	0	0.0	0.0	4	0.00004	0.00004
Deschampsia cespitosa ssp. cespitosa	DECA	0	0.0	0.0	0	0.0	0.0
Botrychium lunaria	BOLU	0	0.0	0.0	4	0.0004	0.0004
Lonicera involucrata	LOIN	0	0.0	0.0	0	0.0	0.0
Number of Plots (n)			24			24	
Species Richness			5.80			7.40	
Total Crown Cover (%)			78.30			104.00	
Dominance Concentration (C)			0.82			0.48	
Diversity (H') (natural logs)			0.43			1.02	

APPENDIX 3-4C
STATISTICAL SUMMARY FOR VASCULAR SPECIES FROM SEADYN ANALYSIS, SERAL STAGES 4 AND 5, SOUTHEAST LYELL SITE

		SERAL STAGE 4 105-145 YEARS (10A & 11B)			SERAL STAGE 5 + 432 YEARS (12A + B)		
SPECIES NAME	VARIABLE	FREQ %	MEAN	STD ERR	FREQ %	MEAN	STD ERR
Abies lasiocarpa	ABLA	83	3.66	1.48	100	11.50	2.85
Pinus albicaulis	PIAL	0	0.0	0.0	0	0.0	0.0
Picea engelmannii	PIEN	100	57.11	7.97	100	51.30	6.87
Populus balsamifera	POBA	92	3.74	1.16	67	19.16	13.35
Pseudotsuga menziesii	PSME	50	0.80	0.61	17	0.18	0.18
Arctostaphylos rubra	ARRU	8	0.32	0.32	50	0.91	0.45
Arctostaphylos uva-ursi	ARUV	83	0.80	0.34	50	0.86	0.68
Chimaphila umbellata ssp. occidentalis	CHUM	67	0.08	0.03	100	0.46	0.15
Dryas drummondii	DRDR	92	4.56	1.98	17	0.002	0.002
Juniperus communis	JUCO	42	0.05	0.03	17	0.02	0.02
Linnaea borealis ssp. americana	LINB	17	0.05	0.04	0	0.0	0.0
Rubus idaeus ssp. melanolasius	RUID	17	0.02	0.02	0	0.0	0.0
Salix barclayi	SABA	50	0.83	0.61	17	0.02	0.02
Salix brachycarpa ssp. brachycarpa	SABR	8	0.07	0.07	0	0.0	0.0
Salix commutata	SACO	0	0.0	0.0	0	0.0	0.0
Salix drummondiana	SADR	42	1.0	0.62	17	0.03	0.03
Salix farriae	SAFA	0	0.0	0.0	33	0.18	0.11
Salix glauca var. villosa	SAGL	91	9.63	3.94	83	4.26	1.87
Salix scouleriana	SASC	8	0.22	0.22	0	0.0	0.0
Salix sp.	SASP	0	0.0	0.0	0	0.0	0.0
Salix vestita	SAVE	58	0.82	0.43	50	0.56	0.38
Shepherdia canadensis	SHCA	100	40.62	3.69	100	40.47	5.02
Anemone parviflora	ANPA	0	0.0	0.0	0	0.0	0.0
Castilleja miniata	CAMI	8	0.0008	0.0008	0	0.0	0.0
Castilleja rhexifolia	CARH	0	0.0	0.0	0	0.0	0.0
Corallorhiza trifida	COTR	33	0.004	0.003	17	0.0002	0.0002
Epilobium angustifolium	EPAN	17	0.04	0.04	0	0.0	0.0
Epilobium latifolium ssp. latifolium	EPLA	0	0.0	0.0	0	0.0	0.0
Erigeron lonchophyllus	ERLO	8	0.004	0.004	0	0.0	0.0
Fragaria virginiana ssp. glauca	FRVI	42	0.09	0.04	0	0.0	0.0
Goodyera repens var. repens & G. oblongifolia	GORE	33	0.05	0.03	33	0.007	0.004
Habenaria obtusata	HAOB	0	0.0	0.0	67	0.09	0.04
Habenaria hyperborea	HAHY	0	0.0	0.0	17	0.005	0.005
Listera borealis	LIBO	58	0.02	0.009	17	0.0008	0.0008
Moneses uniflora	MOUN	42	0.19	0.11	50	0.09	0.05
Orchis rotundifolia	ORRO	0	0.0	0.0	0	0.0	0.0
Orthilia secunda	ORSE	83	0.68	0.18	100	1.80	0.32
Osmorhiza depauperata	OSDE	0	0.0	0.0	17	0.0005	0.32
Oxytropis monticola ssp. monticola	OXMO	0	0.0	0.0	0	0.0	0.0
Pyrola asarifolia	PYAS	58	0.40	0.24	100	2.33	0.86
Pyrola chlorantha	PYCH	67	0.15	0.09	67	0.11	0.06
Agropyron trachycaulum var. trachycaulum	AGTR	0	0.0	0.0	0	0.0	0.0
Agropyron violaceum	AGVI	0	0.0	0.0	0	0.0	0.0
Carex aurea and C. concinna	CAAU	58	0.45	0.21	100	2.67	0.77
Carex eburnea	CAEB	0	0.0	0.0	50	0.50	0.33
Carex sp.	CASP	0	0.0	0.0	0	0.0	0.0
Deschampsia cespitosa ssp. cespitosa	DECA	0	0.0	0.0	17	0.002	0.002
Botrychium lunaria	BOLU	0	0.0	0.0	0	0.0	0.0
Lonicera involucrata	LOIN	8	0.08	0.08	0	0.0	0.0
Number of Plots (n)			12			6	
Species Richness			15.30			14.70	
Total Cover (%)			126.50			137.50	
Dominance Concentration (C)			0.32			0.25	
Diversity (H') (natural logs)			1.55			1.69	
(natural logs)							

APPENDIX 3-5A STATISTICAL SUMMARY FOR NON-VASCULAR SPECIES FROM SEADYN ANALYSIS, SERAL STAGES 2 AND 3, SOUTHEAST LYELL SITE

		SERAL STAGE 2 20-50 YEARS (2A - 5B)			SERAL STAGE 3 50-90 YEARS (6A - 9B)		
SPECIES NAME	VARIABLE	FREQ %	MEAN	STD ERR	FREQ %	MEAN	STD ERR
Amblystegium serpens	AMSE	17	0.004	0.002	50	0.03	0.01
Aulacomnium palustre	AUPA	0	0.0	0.0	0	0.0	0.0
Bryum caespiticium	BRCA	96	0.28	0.05	100	0.77	0.11
Brachythecium groenlandicum	BRGR	100	0.36	0.08	100	0.98	0.18
Brachythecium salebrosum	BRSA	0	0.0	0.0	13	0.007	0.005
Campylium chrysophyllum	CACH	25	0.009	0.006	42	0.02	0.01
Campylium halleri	CAHA	0	0.0	0.0	13	0.004	0.003
Campylium halleri & C. stellatum	CAHS	0	0.0	0.0	0	0.0	0.0
Campylium stellatum	CAST	0	0.0	0.0	0	0.0	0.0
Ceratodon purpureus	CEPU	50	0.04	0.02	79	0.16	0.04
Dicranum acutifolium	DIAC	0	0.0	0.0	0	0.0	0.0
Ditrichum flexicaule	DIFL	88	0.10	0.03	75	0.10	0.03
Dicranum fuscescens & muehlenbeckii	DIFU	0	0.0	0.0	0	0.0	0.0
Dicranum scoparium	DISC	0	0.0	0.0	0	0.0	0.0
Drepanocladus uncinatus	DRUN	75	0.19	0.04	100	0.70	0.11
Eurhynchium pulchellum	EUPU	4	0.002	0.002	33	0.004	0.003
Grimmia apocarpa	GRAP	13	0.001	0.0008	50	0.03	0.01
Hypnum revolutum	HYRE	29	0.001	0.0009	38	0.20	0.07
Hylocomium splendens	HYSP	0	0.0	0.0	75	0.22	0.05
Lescurasa radicosa	LERA	4	0.0008	0.0008	0	0.0	0.0
Minium spinulosum	MNSP	0	0.0	0.0	0	0.0	0.0
Pleurozium schreberi	PLSC	0	0.0	0.0	0	0.0	0.0
Ptilium crista-castrensis	PTCR	0	0.0	0.0	8	0.003	0.003
Pylaisiella polyantha	PYPO	0	0.0	0.0	0	0.0	0.0
Rhytidiadelphus triquetrus	RHTR	0	0.0	0.0	8	0.002	0.001
Thuidium abietinum & T. recognitum	THSP	8	0.007	0.006	25	0.02	0.01
Timmia austriaca	TIAU	0	0.0	0.0	0	0.0	0.0
Tortula norvegica & ruralis	TOSP	79	0.79	0.22	88	0.48	0.11
Tortella tortuosa	TOTO	58	0.12	0.04	88	0.14	0.03
Barbilophozia lycopodioides	BALY	0	0.0	0.0	0	0.0	0.0
Barbilophozia barbata &hatcheri	BASP	0	0.0	0.0	0	0.0	0.0
Lophozia quadriloba, incisa &ventri	LOSA	0	0.0	0.0	0	0.0	0.0
Ptilidium pulcherrimum	PTPU	0	0.0	0.0	0	0.0	0.0
Acarospora spp.	ACSP	8	0.007	0.005	0	0.0	0.0
Baeomyces rufus	BARU	0	0.0	0.0	0	0.0	0.0
Buellia spp.	BUSP	8	0.03	0.02	0	0.0	0.0
Caloplaca sinapisperma	CASI	4	0.0002	0.0002	50	0.02	0.01
Cetraria ericetorum	CEER	0	0.0	0.0	0	0.0	0.0
Cetraria pinastri	CEPI	0	0.0	0.0	0	0.0	0.0
Cladonia arbuscula	CLAR	0	0.0	0.0	0	0.0	0.0
Cladonia cariosa	CLAR	0	0.0	0.0	0	0.0	0.0
Cladonia cariosa	CLCE	0	0.0	0.0	0	0.0	0.0
Cladonia chlorocantha, fimbriata, pocillum and pyxidata	CLCH	0	0.0	0.0	8	0.001	0.001
Cladonia cornuta	CLCO	0	0.0	0.0	0	0.0	0.0
Cladonia gracilis	CLGR	0	0.0	0.0	0	0.0	0.0
Cladonia multiformis	CLMU	0	0.0	0.0	0	0.0	0.0
Cladonia scabriuscula	CLSC	0	0.0	0.0	0	0.0	0.0
Cladonia squamules	CLSQ	0	0.0	0.0	4	0.0002	0.0002
Cladonia rangiferina	CLRA	0	0.0	0.0	0	0.0	0.0
Black crustose rock lichen	CRBL	0	0.0	0.0	8	0.02	0.01
White crustose rock lichen	CRWH	0	0.0	0.0	8	0.01	0.009
Hypogymnia physodes	HYPH	0	0.0	0.0	0	0.0	0.0
Lecidea spp.	LESP	0	0.0	0.0	0	0.0	0.0
Parmeliopsis ambigua	PAAM	0	0.0	0.0	0	0.0	0.0
Pachyospora verrucosa	PAVE	0	0.0	0.0	13	0.002	0.002
Peltigera aphthosa	PEAP	0	0.0	0.0	0	0.0	0.0
Peltigera canina	PECA	0	0.0	0.0	0	0.0	0.0
Peltigera canina var. rufescens	PERU	4	0.002	0.002	4	0.0008	0.0008
Polyblastia spp.	POSP	0	0.0	0.0	4	0.0008	0.0008
Rinodina spp.	RISP	0	0.0	0.0	13	0.002	0.002
Xanthoria elegans	XAEL	0	0.0	0.0	13	0.01	0.009
Marasmius epidryas	MAEP	80	0.007	0.002	80	0.002	0.0005
Polyporus elegans	POEL	0	0.0	0.0	0	0.0	0.0
Number of Plots (n)		24			24		
Species Richness		7.30			12.00		
Total Cover (%)		1.93			3.92		
Dominance Concentration (C)		0.24			0.16		
Diversity (H') (natural logs)		1.78			2.16		

1 Seral Stage 1 (most recent moraine) not represented because it has no non-vasular species.

APPENDIX 3-5B STATISTICAL SUMMARY FOR NON-VASCULAR SPECIES FROM SEADYN ANALYSIS, SERAL STAGES 4 AND 5, SOUTHEAST LYELL SITE

SPECIES NAME	VARIABLE	SERAL STAGE 4 105-145 YEARS (10A - 11B) FREQ %	MEAN	STD ERR	SERAL STAGE 5 +432 YEARS (12A - B) FREQ %	MEAN	STD ERR
Amblystegium serpens	AMSE	100	0.23	0.04	100	0.18	0.04
Aulacomnium palustre	AUPA	0	0.0	0.0	17	0.003	0.003
Bryum caespiticium	BRCA	100	0.94	0.16	100	0.18	0.05
Brachythecium groenlandicum	BRGR	100	4.40	0.54	83	2.40	1.13
Brachythecium salebrosum	BRSA	0	0.0	0.0	0	0.0	0.0
Campylium chrysophyllum	CACH	100	0.22	0.04	100	0.18	0.04
Campylium halleri	CAHA	25	0.08	0.05	67	0.05	0.02
Campylium halleri & C. stellatum	CAHS	17	0.006	0.004	0	0.0	0.0
Campylium stellatum	CAST	17	0.03	0.02	67	0.05	0.02
Ceratodon purpureus	CEPU	58	0.06	0.02	17	0.003	0.003
Dicranum acutifolium	DIAC	8	0.007	0.007	83	0.08	0.06
Ditrichum flexicaule	DIFL	100	2.85	0.79	100	0.87	0.31
Dicranum fuscescens & muehlenbeckii	DIFU	42	0.23	0.14	100	0.43	0.11
Dicranum scoparium	DISC	58	0.26	0.11	100	3.08	0.40
Drepanocladus uncinatus	DRUN	100	3.22	0.40	100	2.42	0.47
Eurhynchium pulchellum	EUPU	0	0.0	0.0	0	0.0	0.0
Grimmia apocarpa	GRAP	75	0.07	0.03	0	0.0	0.0
Hypnum revolutum	HYRE	92	2.03	0.56	50	0.03	0.02
Hylocomium splendens	HYSP	100	7.58	1.91	100	49.68	7.17
Lescurasa radicosa	LERA	8	0.004	0.004	0	0.0	0.0
Minium spinulosum	MNSP	0	0.0	0.0	33	0.004	0.002
Pleurozium schreberi	PLSC	8	0.05	0.05	83	1.38	0.60
Ptilium crista-castrensis	PTCR	33	0.004	0.002	83	0.21	0.12
Pylaisiella polyantha	PYPO	17	0.03	0.02	0	0.0	0.0
Rhytidiadelphus triquetrus	RHTR	50	0.43	0.26	50	0.09	0.06
Thuidium abietinum & recognitum	THSP	58	0.30	0.30	0	0.0	0.0
Timmia austriaca	TIAU	0	0.0	0.0	67	0.01	0.008
Tortula norvegica & ruralis	TOSP	83	0.09	0.04	33	0.03	0.02
Tortella tortuosa	TOTO	92	0.82	0.12	83	0.17	0.11
Barbilophozia lycopodioides	BALY	58	0.05	0.03	100	2.95	0.75
Barbilophozia barbata &hatcheri	BASP	33	0.01	0.007	100	0.22	0.05
Lophozia quadriloba, L. incisa & L. ventri	LOSA	33	0.03	0.02	100	0.16	0.06
Ptilidium pulcherrimum	PTPU	0	0.0	0.0	67	0.25	0.17
Acarospora spp.	ACSP	0	0.0	0.0	0	0.0	0.0
Baeomyces rufus	BARU	25	0.02	0.02	0	0.0	0.0
Buellia spp.	BUSP	42	0.04	0.02	50	0.02	0.01
Caloplaca sinapisperma	CASI	75	0.17	0.05	0	0.0	0.0
Cetraria ericetorum	CEER	17	0.009	0.006	0	0.0	0.0
Cetraria pinastri	CEPI	8	0.0004	0.0004	0	0.0	0.0
Cladonia arbuscula	CLAR	0	0.0	0.0	33	0.01	0.009
Cladonia cariosa	CLCA	100	0.11	0.02	50	0.04	0.02
Cladonia cariosa	CLCE	0	0.0	0.0	100	0.10	0.05
Cladonia chloroantha, fimbriata, pocillum and pyxidata	CLCH	100	0.73	0.17	50	0.06	0.04
Cladonia cornuta	CLCO	0	0.0	0.0	17	0.003	0.003
Cladonia gracilis	CLGR	25	0.02	0.01	50	0.05	0.03
Cladonia multiformis	CLMU	0	0.0	0.0	17	0.005	0.005
Cladonia scabriuscula	CLSC	50	0.13	0.09	0	0.0	0.0
Cladonia squamules	CLSQ	100	2.21	0.39	100	0.41	0.16
Cladonia rangiferina	CLRA	0	0.0	0.0	50	0.02	0.01
Black crustose rock lichen	CRBL	17	0.003	0.002	0	0.0	0.0
White crustose rock lichen	CRWH	0	0.0	0.0	0	0.0	0.0
Hypogymnia physodes	HYPH	0	0.0	0.0	17	0.05	0.05
Lecidea spp.	LESP	17	0.02	0.01	0	0.0	0.0
Parmeliopsis ambigua	PAAM	0	0.0	0.0	17	0.008	0.008
Pachyospora verrucosa	PAVE	0	0.0	0.0	0	0.0	0.0
Peltigera aphthosa	PEAP	17	0.02	0.01	100	0.39	0.18
Peltigera canina	PECA	50	0.52	0.30	100	0.25	0.09
Peltigera canina var. rufescens	PERU	42	0.20	0.12	0	0.0	0.0
Polyblastia spp.	POSP	0	0.0	0.0	0	0.0	0.0
Rinodina spp.	RISP	17	0.12	0.08	0	0.0	0.0
Xanthoria elegans	XAEL	0	0.0	0.0	0	0.0	0.0
Marasmius epidryas	MAEP	25	0.001	0.001	0	0.0	0.0
Polyporus elegans	POEL	8	0.0008	0.0008	0	0.0	0.0
Number of Plots (n)		12			6		
Species Richness		23.00			27.30		
Total Cover (%)		28.30			66.50		
Dominance Concentration (C)		0.13			0.57		
Diversity (H') (natural logs)		2.44			1.20		

APPENDIX 3-6

Species List

Nomenclature for vascular plants follows Moss (1983), for mosses Ireland et al. (1980), for liverworts Stotler and Crandall-Stotler (1977), and for lichens Bird (1978) and Hawksworth et al. (1980). The nomenclature for the two fungi species follows the system used by H.M.E. Schalkwyk of Edmonton. Ms. Schalkwyk is currently completing a checklist of the fungi of Alberta for publication. Voucher specimens of the vascular species are deposited in the University of Alberta vascular herbarium (ALTA), Edmonton, Canada.

Southeast Lyell Site

* = dominant species (for the particular growth-form)
O = found only on older surfaces
Y = found mostly on young surfaces
F = found only in old-growth forest adjacent to terminal moraine
R = rare

Vascular Species

* *Abies lasiocarpa* (Hook.) Nutt.
O,R *Agropyron trachycaulum* (Link) Malte var. *glaucum* (Pease & Moore)
Agropyron trachycaulum (Link) Malte var. *trachycaulum* Packer
Agropyron violaceum (Hornem.) Lange
F,R *Agrostis scabra* Willd.
R *Anaphalis margaritacea* (L.) Benth. & Hook.
Anemone lithophila Rydb.
R *Anemone parviflora* Michx.
O,R *Antennaria umbrinella* Rydb.
Arctostaphylos rubra (Rehder & Wils.) Fern.
Arctostaphylos uva-ursi (L.) Spreng.
O,R *Aster ascendens* Lindl.
O,R *Aster alpinus* L. ssp. *vierhaperi* Onno.
O,R *Aster sibiricus* L.
O *Astragalus robbinsii* (Oakes) A. Gray var. *occidentalis* (S. Wats.)
R *Betula papyrifera* Marsh.
R *Botrychium lunaria* (L.) Sw.
R *Campanula rotundifolia* L.
R *Carex sp.* L.
O *Carex aurea* Nutt.
O *Carex capillaris* L.
O *Carex concinna* R. Br.
O *Carex eburnea* Boott
Carex franklinii Boott
F,R *Carex scirpoides* Michx.
*,Y *Castilleja miniata* Dougl. *ex* Hook.
Y *Castilleja rhexifolia* Rydb.

O *Chimaphila umbellata* (L.) Bart. ssp. *occidentalis* (Rydb.) Hult.
R *Cirsium hookerianum* Nutt.
O *Corallorhiza trifida* Chatelain
R *Cypripedium calceolus* L.
Cypripedium passerinum Richards.
F,R *Deschampsia cespitosa* (L.) Beauv. ssp. *cespitosa* Packer
* *Dryas drummondii* Richards.
Y,R *Dryas integrifolia* M. Vahl
Y,R *Dryas octopetala* L. ssp. *hookeriana* (Juz.) Hult.
R *Elaeagnus commutata* Bernh. *ex* Rydb.
Eleocharis palustris L. R. & S.
Epilobium angustifolium L.
Y *Epilobium latifolium* L. spp. *latifolium* Packer
F,R *Elymus innovatus* Beal
R *Erigeron acris* L. ssp. *politus* E. Fries
R *Erigeron lonchophyllus* Hook.
O *Fragaria virginiana* Duchesne ssp. *glauca* (S. Wats.)
O *Geocaulon lividum* (Richards.) Fern.
O *Goodyera oblongifolia* Raf.
O *Goodyera repens* (L.) R. Br. var. *repens* Packer
Habenaria hyperborea (L.) R. Br.
O *Habenaria obtusata* (Pursh) Richards.
R *Hedysarum boreale* Nutt. var. *mackenzii* (Rich.)
Juniperus communis L.
O,R *Juniperus horizontalis* Moench
F,R *Juniperus scopulorum* Sarg.
O,R *Linnaea borealis* L. ssp. *americana* (Forbes)
O *Listera borealis* Morong
O *Lonicera involucrata* (Richards.) Banks
O *Moneses uniflora* (L.) A. Gray
O *Orchis rotundifolia* Banks *ex* Pursh
O *Orthilia secunda* (L.) House
O,R *Osmorhiza depauperata* Philippi
Oxytropis monticola A. Gray
* *Picea engelmannii* Parry *ex* Engelm.
R *Pinus albicaulis* Engelm.
Pinus contorta Loudon
F,R *Poa alpina* L.
F,R *Poa annua* L.
Populus balsamifera L.
Populus tremuloides Michx.
Potentilla fruticosa L.
Pseudotsuga menziesii (Mirb.) Franco
Pyrola asarifolia Michx.
O *Pyrola chlorantha* Sw.
O *Ribes lacustre* (Pers.) Poir.
R *Rosa acicularis* Lindl.
O *Rubus idaeus* L. ssp. *melanolasius* Focke.
Salix sp. L.
Y,R *Salix arctica* Pallas
Salix barclayi Anderss.
R *Salix barrattiana* Hook.

Y,R *Salix boothii* Dorn
Salix brachycarpa Nutt. ssp. *brachycarpa*
Y *Salix commutata* Bebb
Salix drummondiana Barr. *ex* Hook.
Salix farriae Ball
* *Salix glauca* L. var. *villosa* (Hook.)
Salix scouleriana Barr. *ex* Hook.
Salix vestita Pursh
Y *Saxifraga aizoides* L.
Senecio pauperculus Michx.
* *Shepherdia canadensis* (L.) Nutt.
R *Solidago multiradiata* Ait.
Taraxacum officinale Weber
O *Thalictrum occidentale* A. Gray
F,R *Thuja plicata* D. Don
Trisetum spicatum (L.) Richt. ssp. *spicatum* Packer
R *Zigadenus elegans* Pursh

Streamside and Seepage Vasculars (may also appear in previous list)

Anaphalis margaritacea (L.) Benth. & Hook.
Carex aurea Nutt.
Carex capillaris L.
Carex concinnoides Mack.
Carex eburnea Boott
Carex scirpoidea Michx.
Epilobium latifolium L.
Equisetum arvense L.
Equisetum variegatum Schleich.
Erigeron acris L.
Eriophorum scheuchzeri Hoppe
Habenaria hyperborea (L.) R. Br.
Juncus alpinoarticulatus Chaix
Juncus balticus Willd.
Juncus castaneus J.E. Smith
Parnassia palustris L.
Parnassia parviflora DC.
Polygonum viviparum L.
Salix drummondiana Barr. *ex* Hook.
Salix brachycarpa Nutt. ssp. *brachycarpa* Packer
Salix commutata Bebb
Salix glauca L. var. *villosa* (Hook.) Anderss.
Saxifraga aizoides L.
Senecio pauperculus Michx.
Solidago multiradiata Ait.
Tofieldia glutinosa (Michx.) Pers.
Tofieldia pusilla (Michx.) Pers.

Mosses

Amblystegium serpens (Hedw.) B.S.G.
O *Aulacommium palustre* (Hedw.) Schwaegr.
* *Brachythecium groenlandicum* (C.Jens.) Schljak.
Brachythecium salebrosum (Web. & Mohr) B.S.G.
* *Bryum caespiticium* Hedw.
Campylium chrysophyllum (Brid.) J. Lange
Campylium halleri (Hedw.) Lindb.
O *Campylium stellatum* (Hedw.) C. Jens.
* *Ceratodon purpureus* (Hedw.) Brid.
O *Dicranum acutifolium* (Lindb. & H. Arnell) C. Jens. *ex* Weinm.
O *Dicranum fuscescens* Turn.
O *Dicranum muehlenbeckii* B.S.G.
F,R *Dicranum polysetum* Sw.
O *Dicranum scoparium* Hedw.
Y,R *Distichium capillaceum* (Hedw.) B.S.G.
* *Ditrichum flexicaule* (Schwaegr.) Hampe
* *Drepanocladus uncinatus* (Hedw.) Warnst.
Eurhynchium pulchellum (Hedw.) Jenn.
Grimmia apocarpa Hedw.
Hylocomium splendens (Hedw.) B.S.G.
Hypnum revolutum (Mitt.) Lindb.
Lescuraea radicosa (Mitt.) Monk.
O,R *Mnium spinulosum* B.S.G.
O *Pleurozium schreberi* (Brid.) Mitt.
Ptilium crista-castrensis (Hedw.) De Not.
Pylaisiella polyantha (Hedw.) Grout
Rhytidiadelphus triquetrus (Hedw.) Warnst.
Thuidium abietinum (Hedw.) B.S.G.
Thuidium recognitum (Hedw.) Lindb.
F *Timmia austriaca* Hedw.
Y,R *Tortella fragilis* (Drumm.) Limpr.
* *Tortella tortuosa* (Hedw.) Limpr.
* *Tortula norvegica* (Web.) Wahlenb. *ex* Lindb.
* *Tortula ruralis* (Hedw.) Gaertn., Meyer & Schreb.

Seepage Mosses

Brachythecium spp.
* *Bryum pseudotriquetrum* (Hedw.) Gaernt., Meyer & Schreb.
* *Catoscopium nigritum* (Hedw.) Brid.
Distichium capillaceum (Hewd.) B.S.G.
* *Drepanocladus revolvens* (Sw.) Warnst.
Leptobryum pyriforme (Hedw.) Wils.
Pohlia cruda (Hedw.) Lindb.

Liverworts

(All on older surfaces, especially in old growth forests)

Barbilophozia barbata (Schmid. *ex* Schreb.)
Barbiliphozia hatcheri (Evans) Loeske
* *Barbiliphozia lycopodioides* (Wallr.) Loeske
Lophozia incisa (Schrad.) Dum.
Lophozia quadriloba (Lindb.) Evans
Lophozia ventricosa (Dicks.) Dum.
Ptilidium pulcherrimum (G. Web.) Hampe
Reboulia hemisphaerica (L.) Raddi

Lichens

R *Acarospora spp.* Mass.
O *Baeomyces rufus* (Huds.) Rebent.
Buellia spp. De Not.
Caloplaca sinapisperma (Lam.) Mah. & Gill.
O *Cetraria ericetorum* Opiz
O,R *Cetraria pinastri* (Scop.) S. Gray
O *Cladonia spp.* Hill *ex* Wigg
F *Cladonia arbuscula* (Wallr.) Rabenh.
O *Cladonia cariosa* (Ach.) Spreng.
F *Cladonia cenotea* (Ach.) Schaer.
O *Cladonia chlorophaea* (Floerke *ex* Somm.) Spreng.
F,R *Cladonia cornuta* (L.) Hoffm.
O *Cladonia fimbriata* (L.) Fr.
O *Cladonia gracilis* (L.) Willd.
F *Cladonia multiformis* Merr.
O *Cladonia pocillum* (Ach.) O. Rich.
O *Cladonia pyxidata* (L.) Hoffm.
F *Cladonia rangiferina* (L.) G.H. Web.
O *Cladonia scabriuscula* (Del. *ex* Duby) Nyl.
F *Hypogymnia physodes* (L.) W. Wats.
O *Lecidea spp.* Ach.
Pachyospora verrucosa (Ach.) Mass.
F *Parmeliopsis ambigua* (Wulf.) Nyl.
O *Peltigera aphthosa* (L.) Willd.
O *Peltigera canina* (L.) Willd.
O,R *Peltigera malacea* (Ach.) Funck.
Y *Peltigera rufescens* (Weis.) Humb.
Polyblastia spp. Mass.
F,R *Psoroma hypnorum* (Vahl) S. Gray
Rinodina spp. (Ach.) Gray
F,R *Stereocaulon alpinum* Laur.
Xanthoria elegans (Link) Th. Fr.

Epiphytic Lichens
(All on older trees)

Bryoria spp. Brodo & D. Hawksw.
Caloplaca holocarpa (Hoffm.) Wade
Candelariella spp. Mull. Arg.
Candelariella xanthostigma (Ach.) Lett.
* *Cetraria pinastri* (Scop.) S. Gray
Hypogymnia austerodes (Nyl.) Raes.
* *Hypogymnia physodes* (L.) W. Wats.
Hypogymnia tubulosa (Schaer.) Hav.
Ochrolechia sp. Mass.
Parmelia exasperatula Nyl.
Parmeliopsis ambigua (Wulf.) Nyl.
Parmeliopsis hyperopta (Ach.) Arn.
Pertusaria spp. DC.
Physconia detersa (Nyl.) Poelt
* *Ramalina sp.* Ach.
Usnea alpina Mot.
Usnea cavernosa Tuck.
* *Usnea sorediifera* (Arn.) Lynge.

Fungi

Marasmius epidryas Kuhner
Polyporus elegans Bull. *ex* Fries

Columbia Icefield Site

* - dominant species (for the particular growth form)

Vascular Species

* *Abies lasiocarpa* (Hook.) Nutt.
Achillea millefolium L.
Agropyron trachycaulum (Link) Malte var. *trachycaulum* Packer
Arctostaphylos rubra (Rehder & Wils.) Fern.
Arctostaphylos uva-ursi (L.) Spreng.
Aster sibiricus L.
Calamagrostis montanensis Scribn.
Carex scirpoidea Michx.
* *Dryas drummondii* Richards.
Dryas integrifolia M. Vahl
Dryas octopetala L. ssp. *hookeriana* (Juz.) Hult.
x *integrifolia* M. Vahl
Festuca brachyphylla Schultes
Hedysarum boreale Nutt. var. *mackenzii* (Rich.) C. L. Hitchc.
Juniperus communis L.
* *Picea engelmannii* Parry ex Engelm.

Poa alpina L.
Poa glauca Vahl
Salix arctica Pallas
Salix barrattiana Hook.
Salix drummondiana Barr. *ex* Hook.
* *Salix glauca* L. var. *villosa* (Hook.) Anderss.
Salix reticulata L. ssp. *nivalis* Loeve, Loeve & Kapoor
* *Salix vestita* Pursh
Selaginella densa Rydb.
* *Shepherdia canadensis* (L.) Nutt.

Moss Species

Brachythecium groenlandicum (C.Jens.) Schljak.
Bryum spp. Hedw.
Bryum algovicum Sendtn. *ex* C. Mull.
* *Bryum caespiticium* Hedw.
Bryum capillare Hedw.
Campylium polygamum (B.S.G.) C. Jens.
* *Ceratodon purpureus* (Hedw.) Brid.
Distichium capillaceum (Hedw.) B.S.G.
* *Ditrichum flexicaule* (Schwaegr.) Hampe
Drepanocladus uncinatus (Hedw.) Warnst.
Grimmia apocarpa Hedw.
Hylocomium splendens (Hedw.) B.S.G.
Hypnum revolutum (Mitt.) Lindb.
Hypnum vaucheri Lesq.
* *Tortella fragilis* (Drumm.) Limpr.
* *Tortella inclinata* (Hedw.) Limpr.
Tortella tortuosa (Hedw.) Limpr.
Tortula mucronifolia Schwaegr.
Tortula norvegica (Web.) Wahlenb. *ex* Lindb.
Tortula ruralis (Hedw.) Gaertn., Meyer & Schreb.

Lichens

Caloplaca jungermanniae (Vahl) Th. Fr.
Caloplaca sinapisperma (Lam.) Mah. & Gill.
Caloplaca tetraspora (Nyl.) Oliv.
* *Candelariella terrigena* Raes.
* *Candelariella xanthostigma* (Ach.) Lett.
Cetraria ericetorum Opiz
Cetraria nivalis (L.) Ach.
Cetraria tilesii Ach.
Cladonia spp. Hill *ex* Wigg.
Cladonia chlorophaea (Floerke *ex* Somm.) Spreng.
Cladonia pocillum (Ach.) O. Rich.
Coelocaulon aculeatum (Schreb.) Link
Dermatocarpon cinereum (Pers.) Th. Fr.
Lecanora epibryon (Ach.) Ach.

Lecidea spp. Ach.
Lecidea assimilata Nyl.
Peltigera rufescens (Weis.) Humb.
Physconia muscigena (Ach.) Poelt
Rinodina sp. (Ach.) Gray
Solorina bispora Nyl.
Solorina spongiosa (Sm.) Anzi
Stereocaulon tomentosum Fr.
Xanthoria elegans (Link) Th. Fr.

Fungi

Marasmius epidryas Kuhner